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Population biology and disturbance ecology of a native north American bamboo (Arundinaria gigantea)

Paul R. Gagnon
Louisiana State University and Agricultural and Mechanical College, pgagno1@lsu.edu

POPULATION BIOLOGY AND DISTURBANCE ECOLOGY OF A NATIVE NORTH AMERICAN BAMBOO (*ARUNDINARIA GIGANTEA*)

A Dissertation

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by
Paul R. Gagnon
B.A., Baylor University, 1990
M.F.S., Yale School of Forestry and Environmental Studies, 1998
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DEDICATION

To Heather,
who keeps my head in the clouds
and my feet on the ground

And to the memory of
Carrie Lynn Yoder

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ABSTRACT

This dissertation explores effects of windstorm and fire disturbances on the clonal and reproductive biology of cane (*Arundinaria gigantea* Muhl., Poaceae). In this collection of studies, multiple disturbances interact in complex ways, and some interactions appear only after a substantial lag. One implication of this research is that multiple, interacting disturbances might strongly influence the boundary between monodominant and species-rich plant communities. Cane is the only bamboo native to the United States, and once covered vast areas of bottomlands in the southeastern U.S. in monodominant stands called "canebrakes." The study took place on the Buckhorn Wildlife Management Area in Tensas Parish of northeastern Louisiana, in the Mississippi alluvial valley. Here in 2000 a tornado blew down a large swath of bottomland hardwood forest. The four-year experimental study focused on the effects of windstorm and prescribed fire on cane ramet dynamics, reproduction and regeneration from seed. The effect on cane of a large windstorm-generated gap is accelerated new ramet production and increased ramet density. Cane spreads continually, albeit irregularly. This suggests that cane stands might shift location over time as small forest gaps open and close. The effects of fire on cane are complex, and some may be lasting. In the large wind-generated forest gap, populations of cane ramets grow faster for having been burned. Forest-grown ramet populations decline in the year of fires, but growth rates rebound the next year. Unburned populations decline during the study's final year, but previously burned populations do not, suggesting that fire one year might impart resistance to shocks one or more years later. The dissertation proposes how a sequence of windstorm and fire disturbances might promote natural canebrake formation. The counterpoint is that without periodic disturbances, cane ramet populations decline. The dissertation explores cane reproductive ecology and regeneration, and discusses three critical stages: seed production,

germination and seedling establishment. Cane seeds and seedlings appear to germinate and survive most frequently on sites receiving partial sunlight with a layer of leaf litter. The final chapter describes how these experimental results inform cane restoration, and suggests three pathways by which cane restoration might be achieved.

CHAPTER 1

INTRODUCTION

Objectives

Two objectives motivate this dissertation research, one theoretical and one applied. The first objective is theoretical – to explore the influences on plant communities of multiple ecological disturbances interacting over time. More specifically, this dissertation explores whether and how disturbances might affect the formation and persistence of monodominant communities. The second objective is applied – to describe in detail the disturbance ecology of cane (*Arundinaria gigantea* Muhl., Poaceae), the only bamboo native to the United States, and the subject of increasing restoration interest. To that end, this dissertation explores mechanisms driving cane's clonal and population dynamics, with a specific focus on windstorms and fires as ecological disturbances.

Multiple Disturbances and Monodominant Communities

Species-rich and species-poor communities can persist side-by-side even where there is no apparent edaphic boundary (Hart et al. 1989, Connell and Lowman 1989, Nelson 1994). Different disturbance sequences might favor these very different adjacent plant communities (Myers 1990, Paine et al. 1998, Romme et al. 1998). For example, diverse forest and monodominant bamboo communities co-occur throughout the temperate and tropical world. Such bamboos (Poaceae, tribe Bambuseae) depend on natural disturbances to open forest gaps, which they invade and monopolize (Widmer 1997, Judziewicz et al. 1999). These fast-growing, long-lived clonal species thus persist alongside diverse forests (Nelson 1994, Keeley and Bond 1999). Understanding how disturbances enable vigorous plant colonizers to persist in monodominance is important both in natural ecosystems and where invasives such as cogon grass (*Imperata cylindrica*) and common reed (*Phragmites australis*) are problematic. After disturbances, some plants colonize rapidly, forming dense stands that exclude other species (e.g.,

Caswell and Werner 1978, Platt and Connell 2003). Some gain a competitive advantage after certain disturbances change soil nutrients (e.g., C_4 grasses following fire in tallgrass prairies; Collins 1987, 2000). Other plants are highly flammable and might burn competing shrubs or trees, then grow back vigorously afterward (Mutch 1970, Keeley and Bond 1999, Platt 1999).

Cane and Canebrakes

Cane once formed expansive monodominant stands in bottomlands throughout the southeastern United States. In the 19th century, these canebrakes were widespread, co-occurring with southeastern mixed forests (Platt and Brantley 1997, Judziewicz et al. 1999). Cane still occurs in low densities over much of its previous range, but canebrakes like those described by early explorers are now rare (Platt and Brantley 1997, Judziewicz et al. 1999). By one estimate they have been reduced by 98% (Noss et al. 1995). How did monodominant bamboo stands form alongside diverse forests? Studies of other bamboos suggest that large-scale disturbances might generate conditions favorable for cane (Hughes 1957, Nelson 1994, Widmer 1997). Two such large-scale disturbances are windstorms and fires, which have occurred throughout cane's range for millennia (Marsh 1977, Platt and Brantley 1997).

This dissertation explores the links between clonal monodominance and large natural disturbances. It focuses on effects of windstorm and fire disturbances on bamboo dynamics (i.e. growth, survival and recruitment). The study addresses several general research questions about cane, including: How do windstorms and fires separately affect cane clonal dynamics? Do these disturbances have interacting effects on cane? If so, over what time-frame do these interactions influence cane clonal dynamics? Are cane dynamics different in the small, discrete patches common today than in large, continuous stands like historic canebrakes? Do these potentially interacting disturbances influence bamboo sexual reproduction and regeneration? How might

the influence of disturbance on cane reproduction and regeneration affect distribution of cane genets? More specific experimental hypotheses are presented in several of the following chapters.

An Introduction to the Chapters

The various chapters of this dissertation explore cane disturbance ecology from multiple perspectives. Chapter 2 investigates how clonal growth is different in cane growing under a forest canopy compared with cane growing in a large, wind-generated canopy gap. Clonal growth is defined both as rhizome spread and as changes in ramet (culm) density. Chapter 3 investigates the interacting effects of windstorm and fire disturbances over time on cane clonal growth in both small and large cane stands. Clonal growth is measured both as change in ramet density and as dN/dt. Chapter 4 investigates windstorm and fire effects on cane seed germination and seedling survival. The chapter includes many observations about cane flowering, and elucidates several important stages in cane reproduction and regeneration. Chapter 5 synthesizes results pertaining to cane restoration, both from the previous chapters in this dissertation, and from various outside sources. The chapter is intended for an audience of land managers and restoration practitioners, and it describes three possible pathways for restoring cane. Chapter 6 concludes the dissertation by revisiting important findings from each of the studies contained herein.

CHAPTER 2

RESPONSE OF A NATIVE BAMBOO (*ARUNDINARIA GIGANTEA* MUHL., POACEAE) TO WIND DISTURBANCE

Introduction

Dense, monodominant stands of the bamboo called "cane" (*Arundinaria gigantea* Muhl., Poaceae) were once a prominent feature of bottomlands of the southeastern United States. Many early accounts of these canebrakes described them as covering "thousands of acres" and "often extending for miles" (Platt and Brantley 1997 and references therein). Canebrakes were refuge for many game species, neotropical migratory birds and several cane-obligate butterfly species (Roosevelt 1908, Remsen 1986, Moorman et al. 2002, Platt et al. 2001). Following European settlement, canebrakes declined by an estimated 98%, becoming a critically endangered component of southeastern bottomland forest ecosystems (Noss et al. 1995). Alteration of disturbance regimes (e.g., fire and flooding), overgrazing and systematic plowing of cane lands all contributed to canebrake decline (Platt and Brantley 1997).

The ecological processes that generate large canebrakes remain a mystery – one that limits canebrake restoration and management. Cane still occurs throughout its historic range, but mainly as diffuse stands under forest canopy, and as small scattered patches in canopy gaps and at forest edges (Marsh 1977). Early accounts suggest expansive canebrakes develop primarily in large canopy gaps or under sparse forest overstory (Platt and Brantley 1997). Land office survey notes made in the Lower Mississippi Alluvial Valley indicate that large "windfalls" and other forest openings with sparse trees are common there historically (Tingle et al. 2001). Windstorms, (e.g., tornadoes, hurricanes), ice-storms, fires, river flooding and beaver dams are all likely causes of forest gaps in southeastern bottomlands. Cane dynamics remain unexplored in the low- and high-light environments of forest understory and large canopy gaps. Do large-scale disturbances promote the growth of small, diffuse cane stands into expansive canebrakes?

We hypothesize that cane's spreading clonal structure enables it to persist beneath forest canopy and then respond rapidly to large-scale wind disturbance. Cane is one of many New and Old World bamboos that form large, monodominant stands (Keeley and Bond 1999, Judziewicz et al 1999). Bamboos are giant grasses, and cane has indeterminate rhizome growth that produces both new rhizomes and culms (Judziewicz et al. 1999). Cane's rhizome network spreads outward from the site of germination, so genets tend to increase in area as they grow. Individual rhizomes can grow more than 6 m in a single season (Marsh 1977). In the forest understory between wind disturbances, cane genets could survive as diffuse networks of rhizomes and culms. These rhizomes and bases of culms are likely to survive windstorms, just as they often do fires (Hughes 1957). Where a disturbance generates high light levels, accelerated rhizome and culm production from this underground network could produce a dense canebrake.

We explored responses of cane to wind-disturbance in this study. We quantified patterns of cane clonal growth in two environments within a Louisiana bottomland forest – a large wind-generated canopy gap and surrounding forest understory. We developed four hypotheses based on field observations, anecdotal accounts and work by Hughes (1957, 1966). We proposed that in cane stands within a large canopy blowdown gap 1) production of new culms should be greater, 2) clonal expansion should be greater, 3) culm damage rate should be reduced, and 4) culm size should be reduced compared to cane stands beneath forest canopy. Results enabled us to characterize responses of cane to large-scale disturbances that open southeastern bottomland forest canopies, with ecological implications for bamboos that form large, monodominant stands and for other spreading clonal forest plants.

Methods

Cane still occurs in the bottomland hardwood forests of the Tensas watershed in northeastern Louisiana. Geologically and ecologically part of the Lower Mississippi Alluvial Valley (LMAV), the Tensas watershed has some of the most diverse and productive forest ecosystems in the U.S. (Heggem et al. 1999). Virtually the entire Tensas watershed was once forest, with frequent canebrake inclusions (Roosevelt 1908, Burdick et al. 1989, Tingle et al. 2001). The 20% that remains forested has been subject to selective forestry for many decades (Burdick et al. 1989, Heggem et al. 1999). Although diminished, cane is still abundant in the Tensas watershed, typically along edges of forests and under forest canopy. Small remnant canebrakes are still present in some locations.

We conducted our study in the Buckhorn Wildlife Management Area within the Tensas watershed. The Buckhorn WMA (3640 ha; Tensas Parish) contains soils and plant species characteristic of the LMAV (Kellison et al. 1998). The topography is a series of ridges and swales common in the Tensas watershed (Heggem et al. 1999). Buckhorn soils are slightly acid clays and silty clays that are moderately well drained on ridges and poorly drained in swales (Wycoff 1997). Diverse southern bottomland hardwood forest covers much of the area, with such species as willow oak (*Quercus phellos*), overcup oak (*Q. lyrata*), sweetgum (*Liquidambar styraciflua*), bitter and sweet pecan (*Carya aquatica* and *C. illinoensis*) among others (Wycoff 1997). Prominent understory components include dwarf palmetto (*Sabal minor*), American beautyberry (*Callicarpa americana*), briars (*Rubus* spp.) and cane.

The Buckhorn WMA is a mosaic of closed-canopy forest and numerous small and large gaps of various ages, all surrounded by agriculture fields. We obtained the site history from T. Tuma, Forester for the area with the Louisiana Department of Wildlife and Fisheries. During the 1920s and 30s, the tract was owned and logged by the Fisher Lumber Company, a subsidiary of

General Motors. The forest has regenerated naturally to a canopy height 20-40m, with many trees > 75 cm DBH, in large part a result of high site productivity. Since purchasing the area in 1995, the Louisiana Department of Wildlife and Fisheries has implemented single-tree and group selection silviculture, resulting in numerous small canopy gaps. Multiple severe storms have caused other canopy gaps of various sizes and ages (T. Tuma, pers. comm.).

On November 8, 2000, a large tornado conservatively estimated as F2 on the Fujita scale traveled 25 miles across northeastern Louisiana and crossed the Buckhorn WMA (NWS 2000). This tornado caused major canopy damage within a broad swath running southwest to northeast across the entire WMA. Almost complete canopy destruction occurred within an area approximately 1 km wide and for the 4 km length of the WMA. Most trees were snapped off; the rest were blown over. Approximately 0.5 km on either side of this central area experienced substantial, though not complete, canopy damage. Cane was present within the large blowdown.

Beginning 18 months after the tornado, we studied cane in the blowdown and surrounding forest. We considered the blowdown as a "treatment" and the surrounding forest as a "reference" for measuring changes after wind disturbance. In spring 2002 we located eight plots around the large tornado blowdown and eight more under adjacent forest canopy 0.1 to 2.5 km away from the blowdown. Each plot comprised four 1 m^2 subplots within a separate and discrete stand of cane ranging in size from 11 m^2 to 1355 m^2 (mean = 324 m^2). We extensively searched the blowdown area for discrete cane stands and used all eight located. We also randomly selected eight discrete cane stands under forest canopy from among those meeting the selection criterion. We randomly located one subplot within a stand's interior and the other 3 at stand edges 0^o N, 120^o SE, and 240^o SW from that interior plot. We marked each of the four 1m^2 subplots with a circular galvanized steel hoop anchored to the ground.

We used canopy photos to quantify light levels in forest and blowdown plots. We took the photos 1.5 m above every subplot in late summer 2002 using a Nikon Coolpix 4500 digital camera with an F8 fisheye lens. We estimated percent total transmitted light from these photos using Gap Light Analyzer 2.0 (Frazer et al. 1999). The canopy over forest-grown plots had a mean total transmitted light of 16.1%, which reflected the silviculture practiced on the Buckhorn WMA. In contrast, blowdown plots had a mean total transmitted light of 88.3%, as expected for a very large canopy gap. We compared least square means of percent transmitted light in plots within the two treatments using a heterogeneous variance model and logit-transformed data in Proc Mixed in SAS (SAS Inst. 1999). Differences were significant ($P < 0.01$).

We measured all cane culms in every subplot in February/March of 2003 and 2004. During the second census we recorded how many new culms were produced in the intervening 12 months. Culms reach full height and diameter in a matter of weeks after sprouting from the rhizomes and then live for five or more years before senescing (Hughes 1957). We measured how many times each culm had branched. Culms produce leaves from straight, slender branches that originate at culm nodes. These nodes produce single or double branchings in the culm's first year and then produce new branches from the previous year's branches each subsequent year (Hughes 1957, 1966). Because culm branches grow in this modular way at regular intervals, the order of culm branchings reflects culm age. We noted whether culms were damaged and how that damage was sustained. We also measured culm height and basal diameter. To estimate rate of clonal spread, we delineated the perimeter of every plot during censuses 1 and 2 using a Leica GPS 500 differential receiver with Coast Guard beacon receiver and sub-meter accuracy.

We performed one-way and nested ANOVAs on these data. Plots were our experimental units. We used Proc Mixed and Proc Glimmix in SAS (SAS Inst. 1999, SAS Inst. 2005) to test

for differences between blowdown- and forest-grown cane culms. Where appropriate, we used a binomial distribution with logit transformation or a Poisson distribution with log transformation. We fitted heterogeneous-variance models where necessary (we specify the response variables, procedures and transformations used for each dataset in the Results). We ran linear regressions of culm height on culm basal diameter and of culm height on light level. We used Pearson's chi-square to check homogeneity of proportions for categorical datasets. We used ArcGIS 9.0 ArcMap to calculate area of cane plots. Because the polygons formed by cane plots were highly irregular in shape, we modeled area of polygons as circles. Then, as a measure of mean radial growth, we took differences in the resulting circle radii from the two censuses to estimate rate of clonal spread.

Results

New culm production rates in tornado-blowdown plots were twice those of forest plots over the 12 month study period. On average, plots in the blowdown produced one new culm for every 2.5 culms present, compared to one new culm per 5 culms present in forest plots. Figure 2.1 illustrates the difference calculated as the number of new culms in 2004 divided by the number of pre-existing culms in 2003. This difference supported our first hypothesis and was significant ($P < 0.04$) using Proc Glimmix in SAS with a Poisson distribution and log link.

Cane culms were younger on average in the tornado blowdown than in the forest. At the time of the first census (winter 2003), culms in the blowdown were in disproportionately earlier stage classes than culms in forest plots. There were twice as many young culms (stage 0-2) growing in blowdown plots compared to forest plots (Figure 2.2). Stage is a proxy for culm age and is based on number of times a given culm has branched (Hughes 1957). Culms in stage 0-2 are typically 1 year old or younger. Each higher-numbered stage normally represents one

additional year in culm age. The difference in stage distributions also supported our first hypothesis and was statistically significant (Pearson chi-square = 78.16, $P < 0.01$).

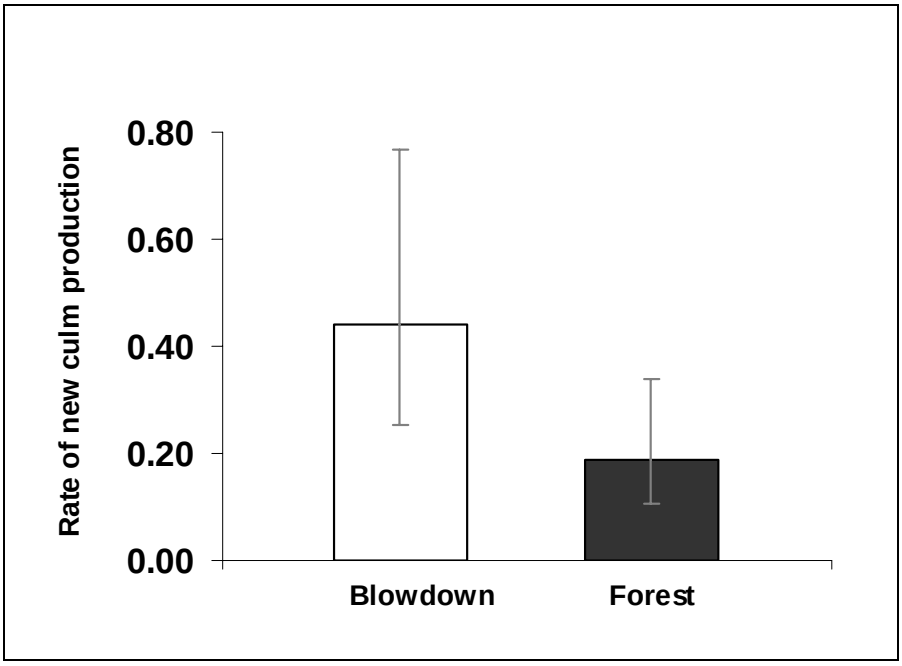

Figure 2.1. Mean rate of new culm production in forest and blowdown. Means are back-transformed least square means. Error bars are back-transformed 95% confidence intervals.

Rate of clonal expansion was not different between tornado-blowdown and forest plots. We were able to calculate reliable shapes and areas for eight blowdown and six forest plots in both years. Rate of radial growth ranged from -0.54 m to 4.68 m. Mean radial growth of forest plots was 1.85 m plus or minus 1.20 m with 95% confidence. Mean radial growth of blowdown plots was 1.50 m plus or minus 1.04 m with 95% confidence. Contrary to our second experimental hypothesis, there was no statistical difference in rate of radial growth between treatments using Proc Mixed in SAS ($P = 0.64$), suggesting that cane rhizomes spread outward regardless of light regime. We also observed that a cane stand might expand several meters in one direction and not at all in another. Such variation in clonal expansion could have produced the highly irregular shapes of cane stands in our study.

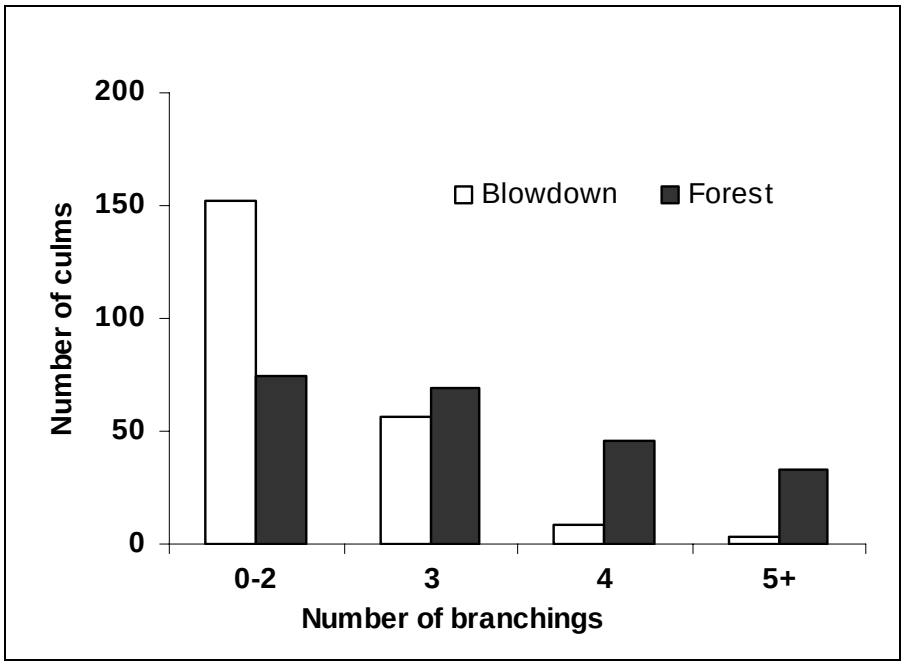

Figure 2.2. Stage distributions of cane culms in forest and blowdown. Stage is determined as the number of branchings present at culm nodes. Counts are based on 220 culms in blowdown plots and 222 in forest plots.

Cane growing in the tornado blowdown was less often damaged or dying than cane growing in the forest. Branches falling from the canopy were the most frequent cause of damage to culms in forest plots. Animals browsing also caused occasional culm damage (typically white-tailed deer {*Odocoileus virginianus*} and swamp rabbits {*Sylvilagus aquaticus*}). By our definition, damaged culms were broken or bent but still alive and green. Some other culms showed no obvious outward damage but were partially dying (these were green from the ground up to some particular node, then dead above that). We observed that in many cases these dying culms were also suffering the effects of branch-falls. Figure 2.3 illustrates that < 10% of the culms in the blowdown were damaged or dying, whereas almost a third of forest-grown culms were damaged or dying. These differences supported our third hypothesis and were significant ($P < 0.01$), based on analysis using Proc Glimmix in SAS with a binomial distribution and logit link.

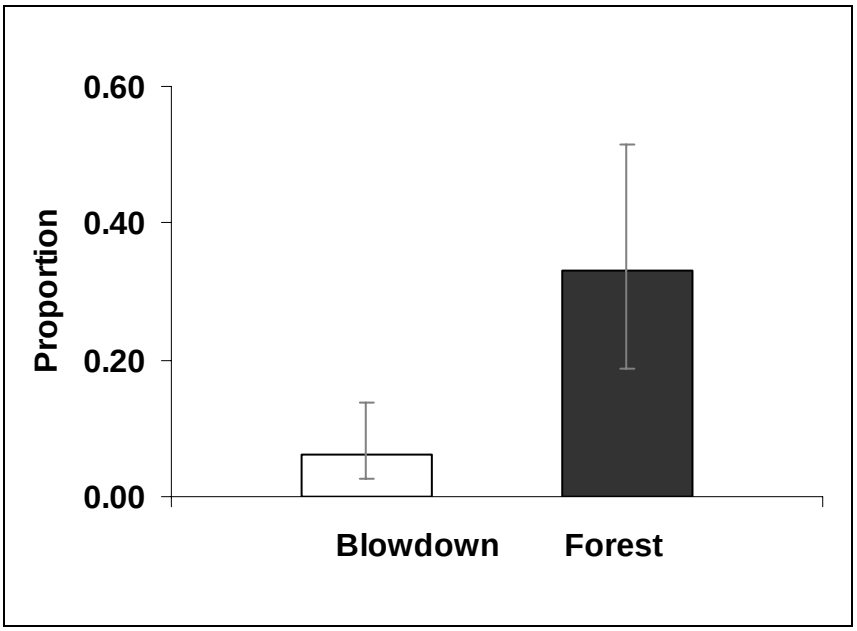

Figure 2.3. Mean proportion of cane culms that are damaged or dying in blowdown and forest plots. Proportions are back-transformed least square means. Error bars are back-transformed 95% confidence intervals.

Culm damage rates were stage related. Older culms were more likely to be damaged or dying than younger culms (Figure 2.4). We examined the first three culm stages from our 2003 census. In support of our third hypothesis, in all three stages culms in tornado-blowdown plots were less likely to be damaged or dying than culms in forest plots (Figure 2.4). Both stage and treatment (forest vs. blowdown) had significant differences ($P < 0.01$ in both cases) using Proc Glimmix in SAS with a binomial distribution and logit link. We excluded the fourth stage (5+) from the figure because there were only 3 surviving culms of this stage in the blowdown. Since all three of these older culms would have survived the tornado, their damage status was directly confounded by the storm itself.

Arundinaria gigantea culms were smaller in tornado-blowdown plots than in forest plots. When we measured them in our late winter censuses, all culms were already full size because

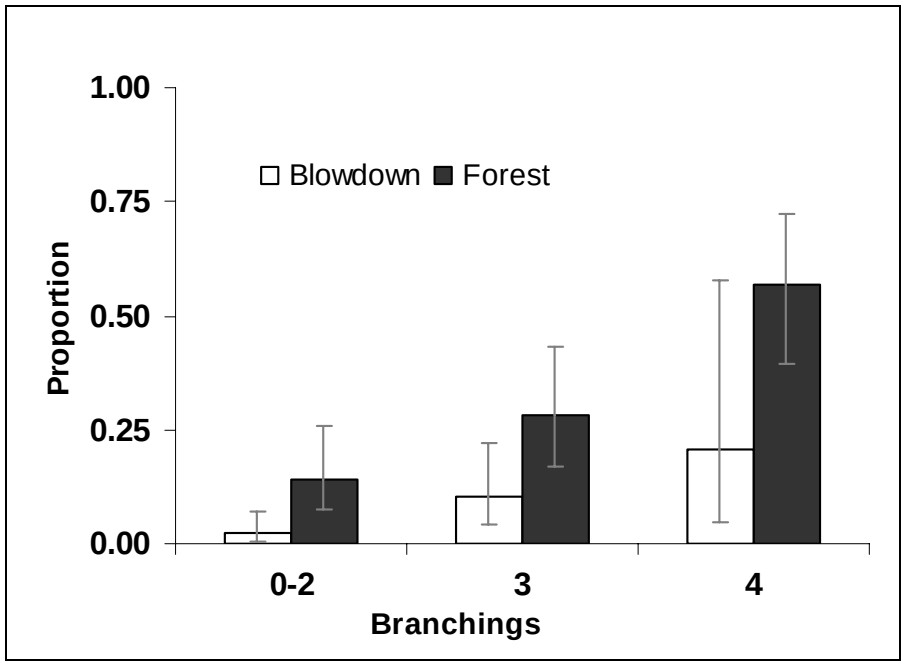

Figure 2.4. Proportion of all culms in given branching classes that were damaged or dying in the blowdown and forest in 2003. Proportions are back-transformed least square means. Error bars are back-transformed 95% confidence intervals.

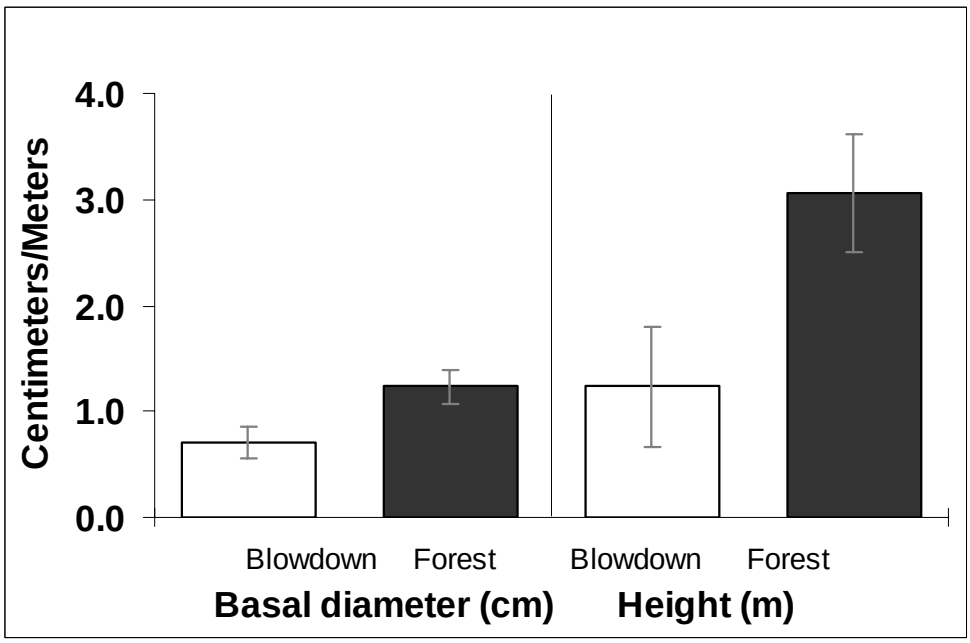

Figure 2.5. Mean culm size of *Arundinaria gigantea* in the blowdown and in surrounding forest. Means are least square means. Error bars indicate 95% confidence intervals.

culms cease growing only weeks after sprouting (Hughes 1957). Culm height in blowdown plots was less than half that in forest plots (Figure 2.5). Similarly, mean basal diameter of culms in blowdown plots was approximately half that in forest plots. Both results supported our fourth hypothesis and were significant using Proc Mixed in SAS ($P < 0.01$). Regression analysis on these two metrics of culm size indicate that height and diameter were tightly linked ($r^2 = 0.84$). Culm height was inversely correlated with transmitted light levels ($r^2=0.54$), meaning culms grew taller in shade than in sun.

Discussion

Cane's quick response to disturbance and likely ability to persist between disturbances are functions of its clonal plasticity. In this study, culm production by cane in the large canopy gap greatly exceeds culm production under forest canopy, signaling rapidly increasing culm density in open-grown cane. We expect culm production to vary with light levels, being greater in gaps and beneath sparse canopy than in full shade. Our results indicate that cane is capable of continual, albeit irregular clonal spread, both in the open and under forest canopy. Hughes (1957, 1966) observed that without periodic disturbances, individual cane stands eventually decline. This implies that cane stands in forests might well shift location over time as canopy gaps open and close. Cane genets might thereby persist for many years beneath overstory trees in old-growth bottomland forests.

Wind disturbance should trigger redevelopment of denser stands. Greatly increased light levels should spark new culm production, while culm damage rates decrease. As they expand, these denser stands are likely to grow together with other stands. Following a windstorm that opens the forest canopy, we thus propose that cane stands that survive the disturbance-free interval might rapidly attain a dense, canebrake-like structure via clonal growth. Historically,

large blowdown gaps are common in the Lower Mississippi Alluvial Valley (Tingle et al. 2001). In Tensas Parish, Louisiana (1,560 km^2) where this study is set, the National Climatic Data Center records 18 tornadoes in the 20 years between 1981 and 2001 (NCDC 2006). Large canopy-dominant trees in bottomland hardwood forests may be more susceptible to wind damage than smaller trees (Glitzenstein and Harcombe 1988). If so, we would expect more and larger canopy gaps, and thus canebrakes, in old-growth than in second-growth bottomland forests.

While increased light levels spur culm production, these new open-grown culms should be smaller than those under forest canopy. In this study, culm height and diameter are inversely related to light level. Hughes (1957) notes a similar trend in cane from the Atlantic coastal plain of North Carolina. In his experimental plots, mean culm size increases each subsequent year after fire. Given the inverse correlation we find between culm height and light level, we hypothesize that new culms grow taller each year following disturbance in response to increasing shade cast by previous years' growth.

Our results suggest the relationship between canebrakes and forest trees are disturbance-driven. Historically, the landscape mosaic of forests and canebrakes would have changed with local small- and large-scale disturbances. Perhaps canebrakes on fertile bottomland soils grow so rapidly that resulting dense cane stands suppress young trees, and thus extend site occupancy by cane for years. Regardless, in the absence of subsequent disturbance, we expect trees to eventually overtop and suppress cane, over time reducing a canebrake to scattered cane stands growing beneath forest canopy.

Cane occurrence and spread in bottomland forests should be limited by environmental barriers. In riverine forests, flooded swales and other sites subject to long-term inundation may act as natural barriers to rhizomatous spread of cane (Marsh 1977). Similarly, new sources of

prolonged flooding (e.g., river meanders, beaver dams) should kill extant cane rhizome networks. Compacted soil, as might occur in floodplains under roads and some skid-trails, could inhibit cane clonal spread (Hughes 1957). Overgrazing is also a potential barrier. Cane is rich fodder for cattle and is susceptible to overgrazing (Hughes 1957). For cane growing in shade at low density, grazing pressure and the trampling that often accompany it could have particularly antagonistic effects. The forest understory beneath dense canopies of regenerating second-growth forests may have reduced local variation in light levels and lower overall transmitted light. Given enough shade for enough time, we expect culm density to decrease slowly and approach zero. Ultimately, cane's shifting cycle of expansion and decline may be limited by its flowering. Like many woody bamboos, cane usually dies after flowering (Hughes 1951, Judziewicz 1999). We expect that both grazing and dense shade will reduce successful pollination and seed production.

Conclusion

Cane's clonal ecology may be a useful model for understanding spreading bamboos and other forest-growing clonal perennials. Our results suggest that cane's rhizome network enables genets to persist under forest canopy by accelerating culm production where light levels increase in small gaps, and senesce as gaps fill-in. Large-scale wind disturbance that opens forest canopy will trigger new culm production. These open-grown culms will be smaller, but grow more densely than under forest canopy. Where present in large disturbance-generated gaps, cane stands could grow together to form extensive canebrakes.

Managers attempting canebrake restoration should consider canopy manipulation if the preferred restoration site is densely forested. Today's younger, managed second-growth forests may be more wind-resistant than old growth forests. If so, fewer and smaller canopy gaps would

offer fewer opportunities for canebrakes to form. Depending on management objectives, smaller gaps created by uneven-aged forestry may be sufficient to increase cane as an understory component.

CHAPTER 3

RAMET POPULATION DYNAMICS AND MULTIPLE DISTURBANCES IN CANE (*ARUNDINARIA GIGANTEA* MUHL., POACEAE)

Introduction

Diverse forest and monodominant bamboo communities co-occur throughout the temperate and tropical world. The bamboos (Fam. Poaceae, tribe Bambuseae) may depend on natural disturbances to open forest gaps, which they invade (Widmer 1997, Judziewicz et al. 1999). These fast-growing, long-lived clonal species can monopolize forest gaps and persist alongside diverse forests (Nelson 1994, Keeley and Bond 1999). Such monodominant bamboo communities are an example of species-rich and species-poor communities persisting side-by-side even where there is no apparent edaphic boundary (Hart et al. 1989, Connell and Lowman 1989, Nelson 1994).

Canebrakes (composed of cane – *Arundinaria gigantea* Muhl.) were monodominant bamboo communities native to North America. In the 19th century, canebrakes were widespread in bottomlands, co-occurring with southeastern mixed forests (Platt and Brantley 1997, Judziewicz et al. 1999). Cane still occurs in low densities over much of its previous range, but canebrakes like those described by early explorers have declined by an estimated 98% (Noss et al. 1995, Platt and Brantley 1997, Judziewicz et al. 1999). How did these monodominant bamboo stands form alongside diverse forests? Studies of other bamboos suggest that large disturbances might generate conditions favorable for cane (Hughes 1957, Nelson 1994, Widmer 1997). Windstorms and fires have occurred throughout cane's range for millennia (Marsh 1977, Platt and Brantley 1997). These two potentially-interacting disturbances may have acted to promote canebrake formation (Hughes 1957 and 1966, Tingle et al. 2001).

We sought to study linkages between bamboo monodominance and large natural disturbances. We modeled bamboo stands as populations of ramets (culms) to explore bamboo dynamics. Specifically, we investigated how cane demography in both small and large stands

was altered by windstorm and fire treatments. We used ramet density and ramet population growth rates (dN/dt) as response variables in a split-plot experimental design to examine the main and interacting effects of windstorm and fire through time. Based on field observations, anecdotal accounts and work by Hughes (1957, 1966), we hypothesized that ramet population growth rates: 1) would be lower in cane stands growing under forest trees than in those located in a large wind-generated canopy gap, 2) would be lower in large, continuous stands than in small, discrete stands, 3) would respond differently to fire depending on whether stands were growing in a large canopy gap or under forest trees, and 4) that disturbances would interact in complex ways over time. Study results suggest how multiple disturbances might interact to form persistent monodominant bamboo stands.

Methods

Study Site

The lower Mississippi alluvial valley was known historically for its expansive canebrakes (Roosevelt 1908, Tingle et al. 2001). Today, cane is still present mainly in small, scattered patches and as widely dispersed culms. River channelization, clearing of bottomland forests for agriculture, repeated intensive logging, and altered fire regimes have all contributed to declines in cane abundance within the lower Mississippi alluvial valley.

We studied cane in the Buckhorn Wildlife Management Area (WMA), in Tensas Parish of northeastern Louisiana (32° 01' N, 91° 22' W). The Buckhorn WMA was previously owned and logged by the Fisher Lumber Company, a subsidiary of General Motors. It has been managed by the Louisiana Department of Wildlife and Fisheries since 1995. The 4,556 ha tract now includes closed canopy second-growth forest and numerous small gaps from wind storms and silviculture operations. A tornado that crossed the tract on November 8, 2000 produced a

large canopy blowdown (see Chapter 2). The resulting forest gap includes a central zone approximately one kilometer wide and 5 kilometers long wherein the forest overstory was almost completely removed.

Stands of cane on the Buckhorn WMA vary in density and continuity. Cane culms frequently occur in small, discrete stands separate from any other cane. When these discrete stands occur in forest, often in small canopy gaps, we denote them "forest stands." When these discrete stands occur in the large tornado-caused canopy blowdown, we denote them "blowdown stands." On the Buckhorn WMA, cane also occurs in continuous stands that cover large areas. The expansive coverage and continuity of these stands are reminiscent of the canebrakes described by early explorers, so we denote these continuous areas of cane "canebrake stands." Often these canebrake stands occur where forest canopy was previously opened by past disturbances. Collectively we refer to these three types of cane stands as "stand states." Forest, blowdown and canebrake stand states each occur under different ages and levels of canopy disturbance.

Experimental Design and Data Collection

We used a split-plot design to test windstorm and fire effects on cane ramet density. This design enabled us to evaluate windstorm and fire main effects, plus any windstorm x fire interaction. The whole-plot treatment was designated as "windstorm" and consisted of the three stand states: forest, blowdown and canebrake stands. We assumed these reflected windstorm-generated canopy conditions. In summer 2002 we randomly chose 30 stands, 10 each of forest, blowdown and canebrake stands. In each stand, we randomly located sets of 4, 1 m^2 sample plots. Using these sets of sample plots, we monitored ramet population growth for two years.

Then we separated the 10 plots in each stand state into 5 pairs matched on the basis of growth rates.

Our split-plot treatment was growing-season fire. We burned one of each pair in forest, blowdown and canebrake stand-states (5 in each stand-state, 15 total). In conjunction with the Louisiana Department of Wildlife and Fisheries, we ignited each of the 15 fire plots separately over a two-day period in April 2004. Each the 15 stands to be burned had a previously cut fire-line around its perimeter. Using a drip torch, we set fires around plot perimeters, so plots burned from perimeter into center. We used data recorders (fireloggers) to monitor fire temperature and duration in each subplot (Grace el al. 2005). We buried a data recorder outside every subplot immediately prior to each prescribed fire, and extended a temperature-sensitive probe into the subplot center. Fireloggers measured temperature at 1-second intervals at an approximate height of 2 cm. We used both calculated and direct-measured metrics of fire characteristics. We analyzed maximum fire temperature and duration as measured by the fireloggers. We calculated total increase in temperature as area under the fire time-temperature curve, after correcting for ambient temperature. We modeled slope of temperature decay from the time-temperature curve using both power and log functions.

We measured density of bamboo culms in 1 m^2 sample plots. We tagged and tracked each cane culm within every 1 m^2 subplot. We noted existing culms, dead culms and new culms during annual late-winter censuses. Using these data, we calculated density of ramets as living culms/m^2. We calculated ramet growth rates based on these annual census data. We defined ramet growth rate as dN/dt, where dN is change in culm density, and dt is change in time. A dN/dt value equal to 1 indicates the population is in stasis because ramet density did not change over time. Values of $dN/dt > 1$ indicate growth, and $dN/dt < 1$ indicate population decline.

We compiled local weather data for this study from the Southern Regional Climate Center. We used data from the nearest weather station, St. Joseph, Louisiana, approximately 18 km southeast of the Buckhorn WMA (SRCC 2006). We used mean monthly rainfall data that began in 1908, the earliest year for which the Southern Regional Climate Center possessed data for St. Joseph.

Analyses

We analyzed data on culm density using analysis of variance and covariance. We used a 3 x 2 split-plot treatment design to test for main effects of windstorm and fire, along with their interaction. We used log-transformation of culm density data to render them normal. We used maximum fire temperature and total increase in temperature (see Appendix A) as covariates for ANCOVA. We also used pre-fire culm density as a covariate in certain analyses. We compared models that assumed either homogeneous or heterogeneous variance but were otherwise identical, and used Chi-square tests of -2 log likelihood to select the better model. In all cases, homogeneous variance models were best. We used SAS Proc Mixed for all culm density analyses (SAS Inst. 1999).

We analyzed data on fire characteristics using a single-treatment mixed ANOVA design. The three stand-states were treatments. We tested effects of stand state on all fire metrics, using maximum temperature and slope of the temperature decay curves as covariates. Chi-square tests of -2 log likelihood indicated that homogeneous variance models were best for all but those using slope decay as the response variable, so we used heterogeneous variance models for those. We performed all analyses of fire characteristics using SAS Proc Mixed.

We analyzed ramet growth rates using analysis of covariance, randomization tests and bootstrapping. We refer to changes in ramet density from one census to the next as “transitions.”

Changes between Censuses 1 and 2 are "Transition 1;" changes between Censuses 2 and 3 are "Transition 2;" and changes between Censuses 3 and 4 are "Transition 3." We used a 3 x 2 split-plot design with repeated measures for ANOVA in SAS Proc Mixed to test for main effects of windstorm, fire, time and their interactions. We used untransformed dN/dt as the primary response variable as these metrics were normal or nearly so, depending on the test. We used maximum fire temperature and total increase in temperature as covariates for ANCOVA. For certain tests, we also used pre-fire culm density or pre-fire dN/dt as covariates. Homogeneous variance models were best according to Chi-square tests of -2 log likelihoods. We used a series of 1000-run randomization tests programmed in R (Venables and Smith, 2006) to test pair-wise hypotheses about significant difference between the various treatment levels (Manley 1997, Caswell 2001). We used 3000-run bootstrapping tests in R to construct 95% confidence intervals around the true means (Caswell 2001).

Results

Ramet Density

Mean ramet density of cane at the Buckhorn WMA changed by treatment over the four year study. It changed little in forest stands, but mean ramet density increased in blowdown stands and decreased in canebrake stands (Figure 3.1). In addition, in the year in which fires occurred, mean ramet density decreased in both burned forest and burned canebrake stands, but increased in burned blowdown stands. Ramet density decreased in all unburned stand states from the third to the fourth censuses (Figure 3.1).

Treatment effects on culm density varied over time. There were no differences among stand-states or between fire treatments at Census 1 (Table 3.1). By Census 3, the first after

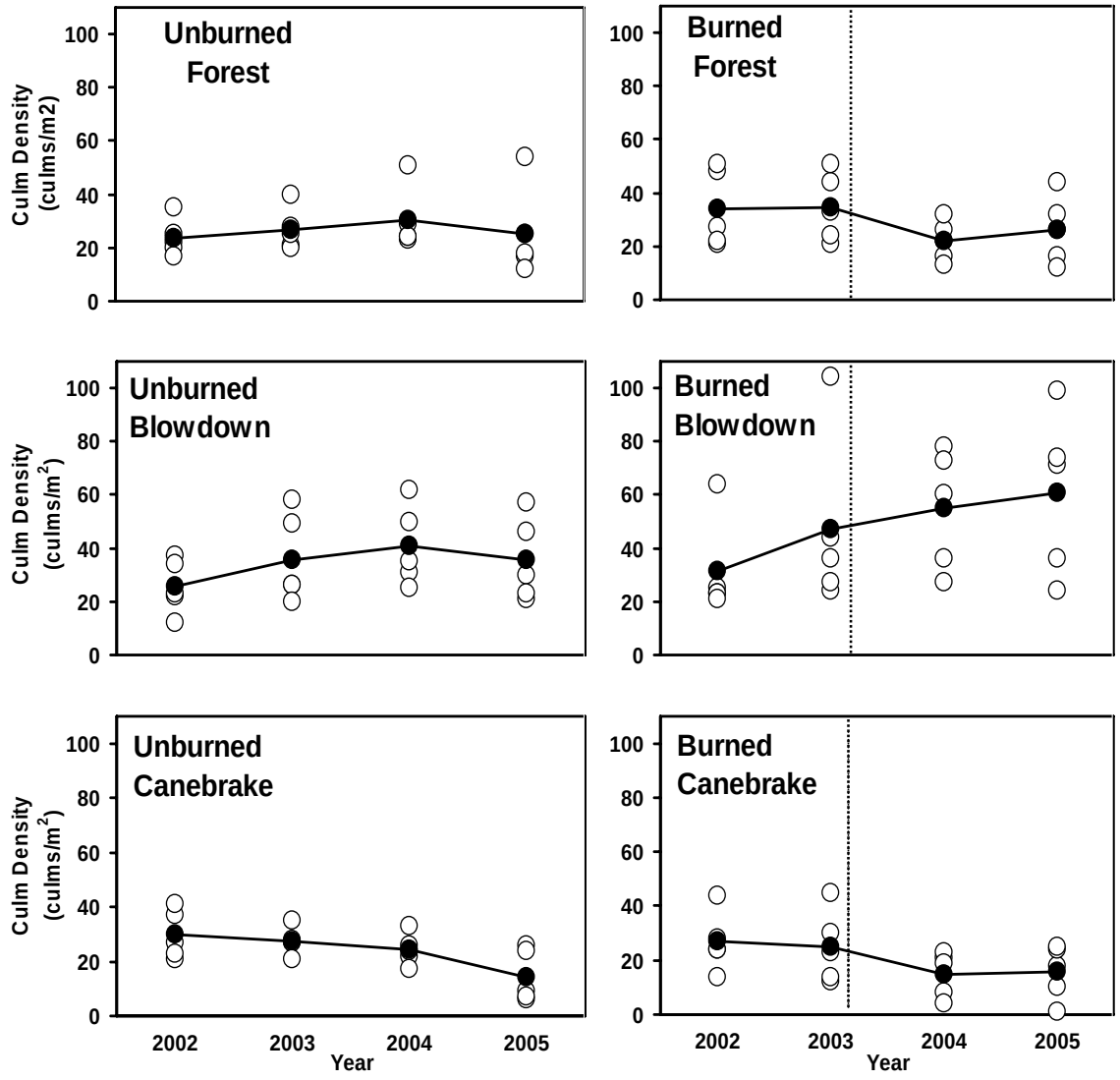

Figure 3.1. Density of bamboo culms across four censuses in each stand type and fire treatment. Open circles represent mean density within a single plot. Filled circles represent mean density in a given year for that combination of burn treatment and stand type. The dotted vertical lines in the burned plots (right side) indicate fires in April 2003.

prescribed fires, there were significant effects on culm density of both stand-state ($p < 0.001$) and fire treatments ($p = 0.029$), but there was no significant interaction effect ($p = 0.108$) (Table 3.1). Orthogonal individual degree of freedom contrasts for census 3 indicated that culm density in blowdown stands differed from that in forest and canebrake stands ($p = 0.041$), but that culm density was similar in forest and canebrake stands ($p = 0.616$) (Table 3.1). Culm density in

census 4 differed by stand-state ($p < 0.001$), but the effect of prescribed fires and of any interaction between stand-state and fire had disappeared (Table 3.1).

Table 3.1. Mixed model ANOVA for culm density (number/m^2) in censuses 1, 3 and 4, with orthogonal individual degree of freedom contrasts. Fire treatment has 2 levels – burned and unburned. Stand-state is a function of wind disturbance and has three levels – forest, blowdown and canebrake. NDF = numerator degrees of freedom; DDF = denominator degrees of freedom based on Kenward-Roger approximation.

Source of Variation:	NDF	DDF	F	*p*
Census 1 Fixed Effects on Culm Density				
Fire (Burned x Unburned)	1	23.8	0.00	0.9944
Stand-State	2	23.8	0.12	0.8907
Fire x Stand State	2	23.8	0.60	0.5554
Individual Degree of Freedom Contrasts				
(Burned x Unburned) x (Blowdown x (Forest+Canebrake))	1	23.9	0.26	0.6130
(Burned x Unburned) x (Forest+Canebrake)	1	23.7	0.94	0.3424
Census 3 Fixed Effects on Culm Density				
Fire	1	27	5.29	0.0294
Stand-State	2	27	19.27	<.0001
Fire x Stand-State	2	27	2.42	0.1084
Individual Degree of Freedom Contrasts				
(Burned x Unburned) x (Blowdown x (Forest+Canebrake))	1	28	4.59	0.0410
(Burned x Unburned) x (Forest+Canebrake)	1	26	0.26	0.6157
Census 4 Fixed Effects on Culm Density				
Fire	1	24.3	0.54	0.4699
Stand-State	2	24.3	11.65	0.0003
Fire x Stand-State	2	24.3	0.10	0.9068
Individual Degree of Freedom Contrasts				
(Burned x Unburned) x (Blowdown x (Forest+Canebrake))	1	25	0.20	0.6615
(Burned x Unburned) x (Forest+Canebrake)	1	23.6	0.00	0.9935

Fire Characteristics and Fire Effects

Stand state influenced the physical characteristics of prescribed fires. According to orthogonal individual degree of freedom contrasts in ANOVA, maximum fire temperatures were higher in blowdown stands than in forest or canebrake stands ($p = 0.047$), and maximum fire temperatures were similar in forest and canebrake stands ($p = 0.433$ in Table 3.2). Total mean

increase in fire temperature was higher in blowdown stands than in the other two stand-states, and differences approached significance ($p = 0.059$ in Table 3.2). Temperature decay and fire duration were not different across stand-states. Because there was a statistical difference in maximum fire temperature across stand-states, we used it as a covariate in the following tests.

Culm density differed among stand-states after plots were burned (Censuses 3 & 4). Culm density differed significantly by stand-state in both years, based on separate ANCOVAs of Census 3 and Census 4 data, ($p = 0.009$ and $p = 0.033$ respectively) (Table 3.3). Post-fire culm density was higher in blowdown than in forest or canebrake stands in both Census 3 and 4 ($p = 0.004$ and $p = 0.020$ respectively in individual degree of freedom contrasts in Table 3.3). Pre-fire culm density predicted post-fire culm density in both Census 3 and 4 ($p < 0.001$ in both cases in Table 3.3).

At first glance, fire effects on growth rates appear transient. During the year of fire treatments (Transition 2), growth rates (dN/dt) differed by stand state ($p = 0.014$ in Table 3.4). Growth rates were different in blowdown stands than in forest and canebrake stands ($p = 0.004$), but not different between forest and canebrake stands (Table 3.4). Pre-fire growth rate was not a good predictor of growth during the year plots were burned ($p = 0.376$). In the year after plots were burned, growth rate no longer differed by stand state ($p = 0.417$), and pre-fire growth rate was a good predictor of post-fire growth ($p = 0.012$ in Table 3.4).

Treatment Effects on Cane Growth from Beginning to End of Study

Overall growth rates in unburned plots differed sharply by stand-state across the four-year study. Figure 3.2 illustrates no net change in the population of cane culms in unburned forest stands between the first and last censuses (dN/dt is not different from 1). The population of cane ramets in blowdown stands grew over the course of the four year study (dN/dt > 1 in

Figure 3.2). The population of cane culms in canebrake stands decreased sharply over the course of the study (dN/dt << 1 in Figure 3.2).

Table 3.2. Mixed model ANOVA for maximum fire temperature and total temperature increase with orthogonal individual degree of freedom contrasts. NDF = numerator degrees of freedom; DDF = denominator degrees of freedom based on Kenward-Roger approximation.

Source of Variation:	NDF	DDF	F	*p*
Fixed Effects on Maximum Temperature				
Stand-State	2	10.3	2.97	0.0957
Individual Degree of Freedom Contrasts				
Blowdown x (Canebrake+Forest)	1	9.34	5.22	0.0471
Canebrake x Forest	1	11.5	0.66	0.4331
Fixed Effects on Total Temperature Increase				
Stand-State	2	12.3	2.20	0.1523
Individual Degree of Freedom Contrasts				
Blowdown x (Canebrake+Forest)	1	11.4	4.39	0.0593
Canebrake x Forest	1	13.4	0.01	0.9177

Table 3.3. Result of mixed model ANCOVA of culm density in burned plots in censuses 3 and 4 using maximum fire temperature and pre-fire culm density as covariates and orthogonal individual degree of freedom contrasts. NDF = numerator degrees of freedom; DDF = denominator degrees of freedom based on Kenward-Roger approximation.

Source of Variation:	NDF	DDF	F	*p*
Census 3 Fixed Effects on Culm Density				
Stand-State	2	12.9	7.02	0.0086
Census 2 culm density (covariate)	1	41.8	20.88	<.0001
Maximum fire temperature (covariate)	1	41.9	1.92	0.1730
Individual Degree of Freedom Contrasts				
(Blowdown x (Forest+Canebrake))	1	13.5	12.06	0.0039
(Forest+Canebrake)	1	12.5	2.40	0.1461
Census 4 Fixed Effects on Culm Density				
Stand-State	2	12.9	4.51	0.0327
Census 2 culm density (covariate)	1	41.4	13.06	0.0008
Maximum fire temperature (covariate)	1	42.0	1.55	0.2200
Individual Degree of Freedom Contrasts				
(Blowdown x (Forest+Canebrake))	1	13.5	6.96	0.0200
(Forest+Canebrake)	1	12.4	2.36	0.1498

Table 3.4. Result of mixed model ANCOVA of culm dN/dt in burned plots in transitions 2 and 3 using pre-fire culm growth rate and maximum fire temperature as covariates with orthogonal individual degree of freedom contrasts. NDF = numerator degrees of freedom; DDF = denominator degrees of freedom based on Kenward-Roger approximation.

Source of Variation:	NDF	DDF	F	*p*
Transition 2 Fixed Effects on Culm Growth Rate				
Stand-State	2	42	4.72	0.0142
Culm dN/dt in transition 1 (covariate)	1	42	0.80	0.3762
Maximum temperature (covariate)	1	42	0.04	0.8406
Individual Degree of Freedom Contrasts				
Blowdown x (Forest+Canebrake)	1	42	9.30	0.0040
Forest x Canebrake	1	42	0.10	0.7487
Transition 3 Fixed Effects on Culm Growth Rate				
Stand-State	2	40	0.89	0.4167
Culm dN/dt in transition 1 (covariate)	1	40	7.00	0.0116
Maximum temperature (covariate)	1	40	1.02	0.3176
Individual Degree of Freedom Contrasts				
Blowdown x (Forest+Canebrake)	1	40	1.69	0.2010
Forest x Canebrake	1	40	0.00	0.9959

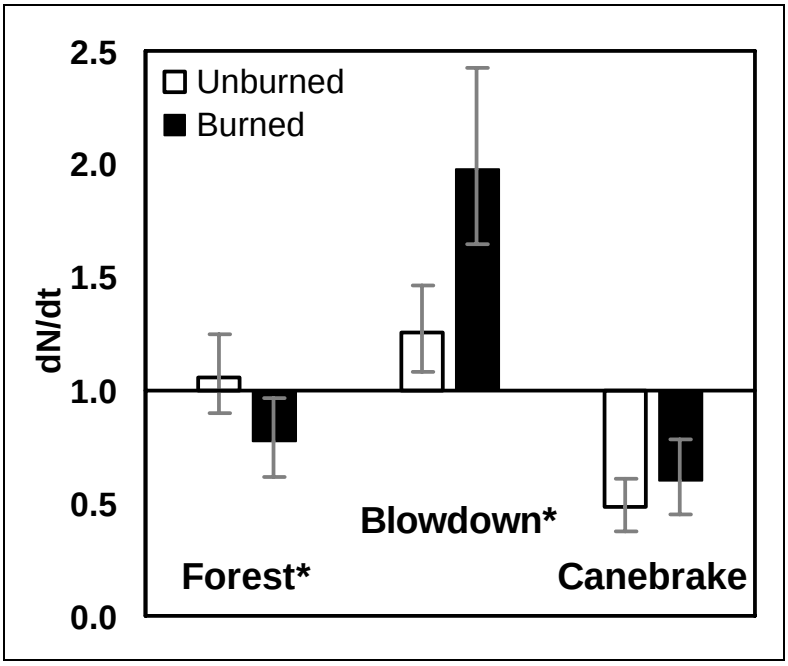

Figure 3.2. Changes in culm density over time (dN/dt) over four years in the different stand states and fire treatments. Values >1 indicate growth, and values <1 indicate decline. Error bars are 95% bootstrapped confidence intervals. Asterisks indicate significant differences between burned and unburned dN/dt of that stand state by randomization tests.

Overall growth rates in burned blowdown plots greatly exceeded those in burned forest or canebrake plots. The population of cane culms in burned forest stands decreased over the course of the four year study, as indicated by $dN/dt < 1$ (Figure 3.2). In contrast during the same period, ramets in burned blowdown stands doubled in number. In burned canebrake stands, the population decrease was similar to that in burned forest stands (Figure 3.2).

Fire affected overall growth rates in forest and blowdown stands but not in canebrake stands. As illustrated in Figure 3.2, which compares Census 4 to Census 1 data, the overall effect of fire treatment in forest stands was a reduced growth rate, from stasis to decline. The effect of fire treatment in blowdown stands was to accelerate an already positive growth rate (Figure 3.2). Fire treatment had no effect on ramet populations in canebrake stands (Figure 3.2).

Individual-Year Treatment Effects on Cane Growth

Cane ramet populations grew at very different rates in different years ($p < 0.001$ in Table 3.5). Orthogonal individual degree of freedom contrasts indicate that growth rates during transition 3 were different from transitions 1 and 2 ($p < 0.001$), and that year 2 growth rates were different from year 1 ($p < 0.001$; Table 3.5). There is a clear fire x transition interaction ($p < 0.001$ in Table 3.5). There is no fire x transition interaction when comparing pre-fire growth rates to growth during the year plots were burned ($p = 0.427$). Rather, the fire by time interaction is prominent during the year after fire (transition 3) compared with the two previous years (transitions 1 and 2) ($p < 0.001$; Table 3.5).

Fire affected growth rates in forest stands both in the year of fire treatment and in the subsequent year. Growth rates in “burned” and “unburned” forest stands were statistically similar before fire treatments (Transition 1) according to randomization tests (Figure 3.3). During the year of fire treatments (Transition 2), growth rates in burned forest stands decreased

and the ramet population shrank (dN/dt < 1 in Figure 3.3), whereas growth rates in unburned forest stands remained unchanged. During the year after prescribed fires (Transition 3.3), growth rates in unburned forest stands decreased and the ramet population shrank (dN/dt < 1 in Figure 3.3). In the same year, growth rates in burned forest stands rebounded from the previous year's low rates and the ramet population increased (dN/dt > 1 in Figure 3.3).

Table 3.5. Result of mixed model ANOVA of dN/dt with repeated measures (transitions) with orthogonal individual degree of freedom contrasts. NDF = numerator degrees of freedom; DDF = denominator degrees of freedom based on Kenward-Roger approximation. BD = blowdown, CB = canebrake, FR = forest, T=transition.

Source of Variation:	**NDF**	**DDF**	**F**	***p***
Fixed Effects on Culm Density				
Transition	2	53.5	17.92	<.0001
Stand-State	2	12.1	6.33	0.0131
Transition x Stand-State	4	54.4	1.31	0.2795
Fire (Burned + Unburned)	1	73.1	1.34	0.2504
Transition x Fire	2	53.6	10.75	<.0001
Stand-State x Fire	2	73.0	1.02	0.3647
Transition x Stand-State x Fire	4	54.4	1.89	0.1261
Individual Degree of Freedom Contrasts:				
Repeated Measures				
(Transition1+Transition2) x Transition3	1	50.4	16.09	0.0002
Transition1 x Transition2	1	63.2	15.08	0.0002
Stand-State				
Blowdown x (Canebrake+Forest)	1	11.9	9.24	0.0104
Canebrake x Forest	1	12.3	3.42	0.0884
Stand-State x Fire				
(Blowdown x (Canebrake+Forest)) x (Burned x Unburned)	1	70.9	1.74	0.1919
(Canebrake+Forest) x (Burned x Unburned)	1	75.3	0.31	0.5808
Repeated Measures x Fire				
((Trans1+Trans2) x Trans3) x (Burned x Unburned)	1	50.5	21.51	<.0001
(Trans1 x Trans2) x (Burned x Unburned)	1	63.2	0.64	0.4270
Repeated Measures x Stand-State x Fire				
((T1+T2) x T3) x (BD x (CB+FR)) x (Burned x Unburned)	1	48.7	5.71	0.0208
((T1+T2) x T3) x (Canebrake+Forest) x (Burned x Unburned)	1	52.3	0.00	0.9871
(T1+T2)) x (BD x (CB+FR)) x (Burned x Unburned)	1	61.0	2.49	0.1199

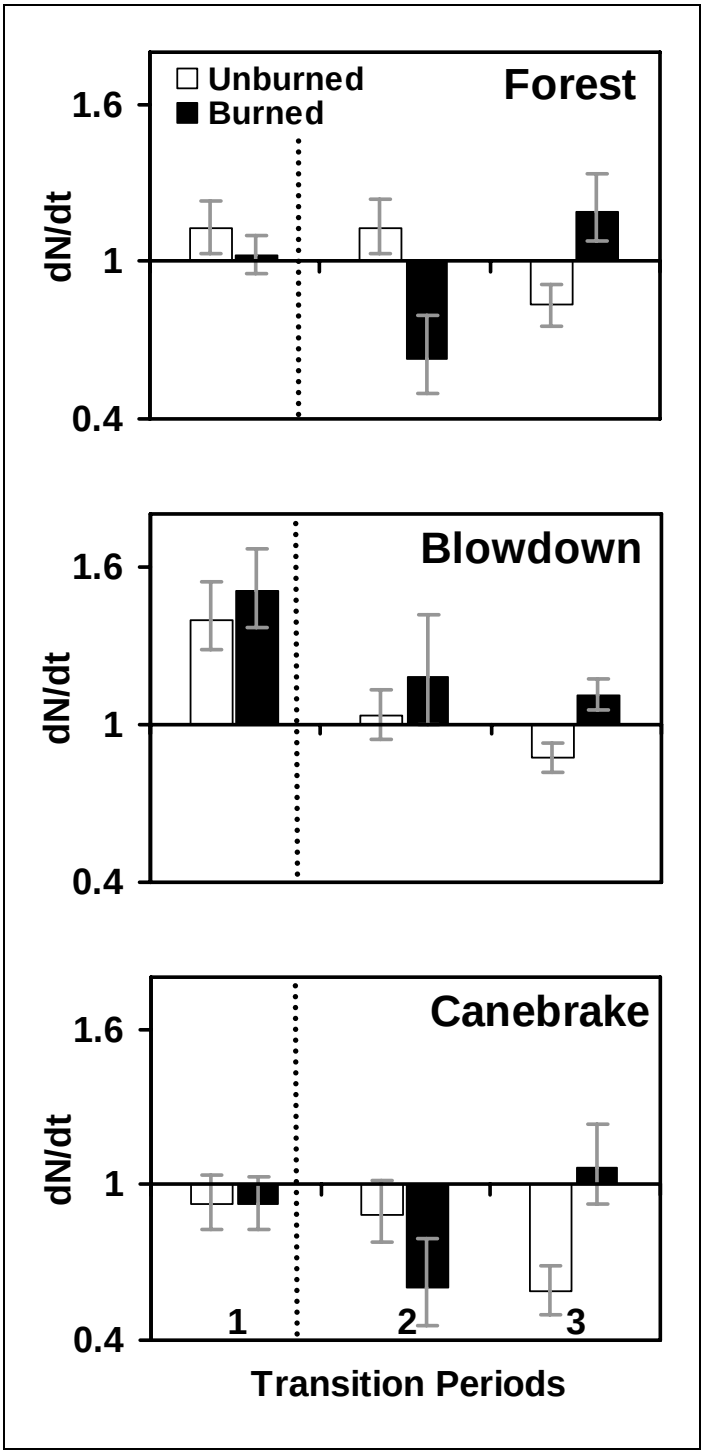

Figure 3.3. Growth rate (change in culm density over time [dN/dt]) for each of three one-year transitions for each stand-type and fire treatment combination. Values >1 indicate growth, and values <1 indicate decline. Error bars are 95% bootstrapped confidence intervals.

Following fires, growth differed in burned and unburned blowdown plots. During the year before fire treatments (Transition 1), growth was strongly positive ($dN/dt >> 1$) and did not significantly differ between "burned" and "unburned" blowdown stands (Figure 3.3). During the year of prescribed fires (Transition 2), growth declined in both, and growth rates were similar in burned and unburned plots (Figure 3.3). During the year after the prescribed fires (Transition 3), growth rates decreased again in unburned blowdown stands and the ramet population shrank ($dN/dt < 1$ in Figure 3.3). In comparison in burned blowdown stands, growth rate increased and so did the ramet population ($dN/dt > 1$ in Figure 3.3).

Growth rates in canebrake stands followed a pattern similar to growth in forest stands, but were lower. During the year before fire treatments (Transition 1), ramet populations in both "burned" and "unburned" canebrake stands were in stasis ($dN/dt \approx 1$), and rates did not differ between the two (Figure 3.3). During the year plots were burned (Transition 2), growth rate did not change in unburned canebrake plots while growth rate and the ramet population decreased in burned canebrake plots ($dN/dt < 1$ in Figure 3.3). During the year after prescribed fires (Transition 3.3), growth rates decreased and the ramet population shrank substantially in unburned canebrake stands ($dN/dt << 1$ in Figure 3.3), while growth rate increased and the ramet population returned to stasis in burned canebrake plots ($dN/dt \approx 1$).

Fire treatment appeared to interact with time in the final year. In Transition 3, populations of all three unburned stand-states declined ($dN/dt < 1$ in Figure 3.3). In contrast, populations increased in two of the three burned stand-states, with the third in stasis ($dN/dt > 1$ for blowdown and forest, $dN/dt \approx 1$ for canebrake in Figure 3.3).

Discussion

Wind disturbance and fire treatments strongly influenced the dynamics of cane ramet populations. Dynamics were very different among the three levels of our windstorm treatment – forest, blowdown and canebrake states. In general, ramet populations of unburned forest stands were in stasis during the four-year study period. During this same time, ramet populations of unburned blowdown stands grew, and ramet populations in unburned canebrake stands declined. Forest and canebrake ramet populations declined during the year of fire treatment; plots simply did not produce as many new culms as were destroyed in the fires. This was not true in blowdown stands, where new culm production in that year surpassed the number destroyed in fires. Growth rates rebounded in forest and canebrake stand-states during the year after the fires.

A fire treatment x time interaction manifested during the study's final year – a one year lag after fire treatment. Repeated measures analysis indicated a fire x time interaction occurred, and *a priori* contrasts indicated fire effects were different in the study's third transition compared with the previous two (Table 3.5). Randomization tests of individual year growth rates offer clues about this interaction. Growth rates were negative during Transition 3 in all three unburned stand-states, whereas populations in two of the three burned stand-states grew (forest and blowdown) and were in stasis in the third (canebrake) (see Figure 3.3). Burned cane stands thereby appeared resistant to whatever caused the decline in unburned stands during the third transition.

We surmise that drought caused the decline of ramet populations in unburned stand-states during Transition 3. Rainfall data for northeast Louisiana from the Southern Regional Climate Center indicate a major drought occurred during 2005 (i.e., Transition 3) (see Appendix B). The St. Joseph weather station, 20 km east of the Buckhorn WMA, recorded a rainfall deficit every month of 2005 except for August and September (Appendix B), when hurricanes Katrina and

Rita both passed through the area. We believe the 2005 drought to be the most likely cause of ramet population decline in unburned cane stands. If true, this would suggest that fire in the year before drought made cane resistant, as evidenced by the fact that ramet populations in previously burned stands either grew or were in stasis despite the drought. We propose that burning replaces weaker, senescing older culms with a cohort of vigorous new ones, and that these young culms (and their underlying rhizomes) are resistant to such environmental shocks as drought.

In general, our findings concur with the only other experimental study published on disturbance and cane. Hughes (1957, 1966) studied switch cane (*A. gigantea*, subsp. *tecta*) near the Atlantic Coast of North Carolina. In keeping with our results, Hughes observed that cane ramets grew denser in the open than under trees. Hughes' major conclusion was that fires rejuvenate stands of cane that typically decline unless periodically burned. That Hughes' findings essentially agree with our own, despite that he studied a different subspecies of cane on the far side of cane's range, suggests that our results may be generalizable to a wide range of habitats across cane's range.

We describe one process by which occasional cane stands might naturally amalgamate to form dense and expansive canebrakes. The first step is for a large-scale disturbance such as hurricane, tornado, ice storm or violent thunderstorm to destroy the forest canopy over a large area where cane is already present in the form of occasional, low-density stands. In the years following such a disturbance, this large blowdown gap is likely to fill-in with very dense vegetation, including expanding cane stands of increasing ramet density. The next step is for fire to occur in this large blowdown gap. Natural fire sources in the form of lightning strikes are abundant throughout the southeastern U.S. (Goodman and Christian 1993), and the dense, regenerating vegetation in a large canopy gap might be an ideal fuel bed. The resulting intense

wildfire would likely damage surrounding forest, thereby enlarging the initial gap. Our results demonstrate that open-grown cane thrives when burned, and that burning may render cane stands more resistant to environmental shocks. We would expect cane in this burned gap to simultaneously expand in area (see Chapter 2) and increase in density. Cane stands might thus amalgamate to form canebrakes. By increasing in size and density, the canebrake would likely grow more pyrogenic as well, potentially increasing fire return interval. Our observations on the Buckhorn WMA demonstrate that the above scenario is by no means far-fetched in the lower Mississippi alluvial valley – large canopy disturbances and lightning strikes are both relatively common occurrences. As some have suggested, anthropogenic fires could facilitate the process of canebrake formation and persistence (Platt and Brantley 1997); however, we believe that persistent and expansive canebrakes could have formed independent of human influence.

This study has shown that multiple ecological disturbances can interact in complex and perhaps unpredictable ways. Results of the study demonstrate that disturbance effects on plant populations depend in part on the disturbance histories of those populations (for another example, see Kwit and Platt 2003). In our study, fire disturbance affected cane ramet populations differently when those populations had already been previously influenced by wind disturbance. Results suggest that previously burned cane populations were resistant to a subsequent disturbance (drought) relative to unburned ramet populations. We propose that in burned stands, the cohort of new ramets replacing older burned culms was more vigorous, and therefore resistant to environmental stresses like drought. We describe how species-rich forests and monodominant canebrake communities might come to persist adjacent to each other, held in place by bifurcated disturbance regimes reflecting different fire frequencies.

CHAPTER 4

REPRODUCTIVE AND SEEDLING ECOLOGY IN A NATIVE NORTH AMERICAN BAMBOO (*ARUNDINARIA GIGANTEA* MUHL., POACEAE)

Introduction

Most woody bamboos are semelparous. They grow vegetatively for decades before flowering and dying (McClure 1966, Judziewicz et al. 1999). The one life stage easily observed in woody bamboos is that of the vegetative "adult." The infrequency of flowering and inconspicuousness of seedlings make studying these life stages difficult. For this reason, flowering, seed germination and seedling growth are poorly documented in many bamboo species (Judziewicz et al. 1999). This is true of cane (*Arundinaria gigantea* Muhl, Poaceae), the bamboo native to North America.

Current understanding of reproductive and seedling ecology in cane are at best incomplete. Accounts of cane flowering vary widely, from reports of occasional culms flowering yearly, to synchronized mass flowering events that produced large quantities of seeds and massive die-offs (Hughes 1951, Marsh 1977, Platt and Brantley 1997 and references therein, Judziewicz et al. 1999). The ecology surrounding cane regeneration from seed is also poorly understood (but see Hughes 1951, Marsh 1977 and Cirtain 2004). Little is written about how post-disturbance conditions influence seed germination and seedling survival in this species for which disturbance is thought to be very important (Platt and Brantley 1997).

We performed the following study to elucidate cane reproductive and seedling ecology. We ran experiments and recorded observations as means of accomplishing two goals. First, we sought to identify and describe critical stages in cane sexual reproduction. Second, we sought to determine the effects of post-disturbance conditions on cane reproduction. Based on our population study of adult cane culms (see Chapter 3), we expected cane seedlings would perform better in high light, previously disturbed environments. We proposed four experimental hypotheses: 1) rate of germination would be higher in post-windstorm conditions (i.e., in a large

forest gap) compared with under forest canopy, 2) rate of germination would be higher in post-fire environments compared with unburned areas, especially where windstorm had also occurred, 3) rate of seedling survival would be higher in post-windstorm conditions compared with under forest canopy, 4) rate of seedling survival would be higher in post-fire environments compared with unburned areas, especially where a windstorm had previously occurred. Windstorms and fires have already been shown to influence cane's "adult" vegetative stage (Hughes 1957, Chapters 2 and 3); this study will address whether windstorms and fires similarly influence cane seed germination rates and seedling survival rates.

Methods

Study Locations

Our primary study site is the Buckhorn Wildlife Management Area in northeast Louisiana. The Buckhorn WMA is located within the lower Mississippi alluvial valley and is administered by the Louisiana Department of Wildlife and Fisheries. The holding comprises 5,000 ha. Approximately three-quarters of this area are under bottomland hardwood forest, while the balance is reclaimed agriculture fields currently undergoing reforestation. The holding was once owned by the Fisher Lumber Co., a subsidiary of General Motors. The area is now managed using single-tree and group selection silviculture. In November 2000, a large F2 tornado traveled 25 miles across northeast Louisiana (SRCC), crossing the Buckhorn WMA and leaving a very large canopy-blowdown gap. The central zone of this gap is approximately 1 km wide and is several kilometers long, through the entire holding. Within this area virtually all forest trees were either snapped off or blown over – the area is almost completely open (see Chapter 2). Cane occurs over much of the Buckhorn WMA along forest edges, under tree canopies and in the large, open tornado blowdown.

A second study site was Tunica Hills Wildlife Management Area, located on bluffs immediately east of the Mississippi River in the "Loess Hills." Tunica Hills WMA includes mixed mesophytic hardwood forests on fertile silt loam soils (Delcourt and Delcourt 1974). Cane was a prominent understory and edge component at Tunica Hills.

Observations of Cane Flowering, Seeding, Germination and Establishment

We visited the Buckhorn WMA every winter and spring for 4 years to document patterns of cane flowering and seed production. We recorded the presence of flowering individuals within patches, and made note of the size of patches. We also looked for seeds on synflorescences whenever flowering individuals were observed, and we checked the ground for seedlings. When we found seeds, we examined them for seed predators. We planned germination trials in the event we were able to collect sufficiently high numbers of seeds.

In spring 2004 we learned of cane flowering en masse at Tunica Hills WMA. This event was different from the ones we observed at Buckhorn. Cane flowered synchronously over a large area, producing a very large quantity of well-developed seeds. On April 22, 2004 we collected approximately 2,000 of these seeds by shaking them from culms, with the intention of using them in field experiments on the Buckhorn WMA. Afterwards, we continued to monitor cane seedling growth at Tunica Hills. We censused the area at the beginning of the next growing season (44 weeks after collecting the seeds), and again one year later (96 weeks after collecting seeds). During this later census, we randomly established eight, 1 m^2 sampling plots up-slope and on ridge-tops in the area. In addition, we excavated one down-slope area of high seedling density and estimated number of stems per rhizomatous individual.

Seed and Seedling Experiments

To estimate the viability of seeds, we performed a series of three germination tests. The day after collecting, we placed 21 well-developed seeds on a moist paper towel and kept them at room temperature. Well-developed seeds were easily distinguished from smaller seeds by their greater size and weight. Six days after harvesting the seeds we randomly chose 90 cane seeds and planted them into a sterile 2:1:1 mix of peat moss, perlite and vermiculite. Four weeks after collecting seeds, we chose 100 well-developed seeds and planted those into a sterile 2:1:1 mix of peat moss, vermiculite and fertilized perlite.

We performed seed experiments to assess the impact of disturbance on cane regeneration. We used a 2 x 2 factorial design on the Buckhorn WMA to test the effects of windstorm, fire and their interaction on cane seed germination and seedling survival. We set up eight study plots in the large tornado blowdown (windstorm treatment) and eight under surrounding forest canopy (windstorm control). Half the plots in each habitat had been burned three weeks prior to planting seeds (fire treatment). We chose only well developed seeds for the experiment. We planted 32 seeds into each of two subplots within every plot by pressing seeds lightly into the soil or leaf litter. We marked the location of every seed using flags, and recensused the plots 3, 11, 44 and 96 weeks after planting. We collected data on germination, establishment, survival and growth of each seed/seedling. We also observed the size and health of seeds and seedlings, and noted any signs of seed predation. We used "overall survival" to refer to the number of living seedlings at study end, 96 weeks after planting. This variable combined germination with seedling establishment and survival. We used "seedling survival" to refer specifically to the likelihood of seedlings in one census surviving to the next census.

Statistical Analyses

We tested for fire and windstorm effects on germination and seedling survival using generalized linear mixed models. We coded germination as a binary response variable weighted by the number of seeds originally planted into each subplot (32). We ran repeated measures analyses on survival, which we calculated as the number of seedlings alive during a given census weighted by number of seedlings alive during the previous census. Our four censuses yielded data for 3 transition periods as the repeated measures (time) variable. We performed these analyses using a binomial distribution and logit link in SAS Glimmix Procedure. This produced a series of odds ratios, which compare the odds of germination or survival among treatment combinations. In addition to the linear model analyses, we explored among-plot differences by ranking plots, and by determining individual plot contributions to overall means.

Results

Observations of Cane Flowering, Seeding, Germination and Establishment

At our primary research site we observed cane flowering during each of four years. Typically, cane commenced flowering in late winter, at which time leaves began to brown and dry. By March, straw-colored flowering patches grew increasingly obvious as the surrounding non-flowering cane began to flush new leaves. On close inspection cane synflorescences resembled large heads of wheat or rice. On multiple occasions we noted a single cane culm flowering alone. Every year small patches of cane, presumably individual genets, flowered but did not produce seed. On two occasions we found patches of cane that flowered a second year but produced no seeds in either year. Twice during the four years we found larger areas of flowering cane that did produce a very limited number of seeds. These few seeds did not dehisce quickly, and we observed several different insects consuming the seeds, including weevils

(Curculionidae), chinch bugs **(***Blissus* sp., family Lygaeidae**)** and a small larva that burrowed through the seeds (Lepidoptera), eating them from the inside. Too few seeds were produced for germination experiments (fewer than two per culm). Flowering culms always died, sometimes after a one-year lag.

In Tunica Hills, most cane synflorescences appeared filled-out with fertile seeds when we first visited the site in early April 2004. Individual culms were laden with scores or even hundreds of seeds. By mid April, the majority of the seed crop had already dropped to the ground, apparently during a storm system that crossed the area just prior. The remaining seeds dehisced readily, and synflorescences fractured in even a light breeze. All adult culms were dead or dying.

Cane recruited abundantly following the mass flowering event. Forty-four weeks after cane dropped its seeds, we observed approximately 12 new seedlings within a 1 m radius of each dead adult culm on hilltops. Seedling density was strongly affected by local topography. Density was lowest on hilltops and much higher down-slope, where seeds were apparently washed by rain. We performed a more thorough seedling census one year later, 96 weeks after cane dropped its seeds. Seedlings remained green through the winter, and we observed many new stems in late February, suggesting seedlings photosynthesized actively well before the forest overstory flushed spring leaves. On hilltops in the area of the flowering event, seedling density averaged 24 stems/m^2. We estimated this represented 7 genets/m^2, as seedlings were already highly rhizomatous. Down-slope on level ground from a typical high-density location we counted approximately 350 stems/m^2. We excavated one, 1 m^2 subplot to examine rhizome structure. We determined that the 350 above-ground stems represented 80-100 separate genets, each with 3-5 above-ground stems.

Seed and Seedling Experiments

A large majority of cane seeds proved fertile in our simple germination tests. When left on a moist paper towel immediately after seed harvest and stored at room temperature, 20 of 21 (95.2%) full-size seeds germinated. When planted 10 days after seed harvest into sterile potting mix, 74 of 90 (82.2%) seeds unsorted by size germinated. When planted into sterile potting mix four weeks after seed harvest, 88 of 100 (88.0%) full-size seeds germinated.

Seeds in burned plots germinated less frequently than seeds in unburned plots. However, this proved to be a weak effect overwhelmed by strong among-plot variation (for fire treatment, $p = 0.09$) (table 4.1). Odds ratios indicate four-fold lesser odds of a seed surviving and germinating in burned blowdown plots than in either burned or unburned forest plots (table 4.2).

Table 4.1. Effects of stand-state, fire and their interaction on rate of germination. Germination is modeled as a binary variable weighted by number of seeds planted per subplot. Analysis used logit transformation in SAS Proc Glimmix.

Source of Variation:	NDF	DDF	F	*p*
Fixed Effects on Cumulative Germination				
Windstorm (forest vs. blowdown)	1	10.67	3.46	0.0906
Fire (burned vs. unburned)	1	10.67	0.97	0.3473
Windstorm x Fire	1	10.67	1.05	0.3280

Table 4.2. Odds ratios of cane seed germination comparing the various treatment combinations. Upper CL and Lower CL are upper and lower 95% confidence limits.

Logit Modeling of Germination:	Odds Ratio	Upper CL	Lower CL
Burned blowdown to unburned blowdown	0.371	0.078	1.772
Burned blowdown to burned forest	0.241	0.051	1.133
Burned blowdown to unburned forest	0.246	0.052	1.157
Unburned blowdown to burned forest	0.648	0.140	3.010
Unburned blowdown to unburned forest	0.662	0.143	3.074
Burned forest to unburned forest	1.021	0.223	4.679

Germination of cane seeds in our field experiment varied strongly among plots. Seeds appeared vulnerable to seed predators – probably rodents and/or birds. During our first two censuses, we found evidence (i.e., the stripped off bracts) that many seeds that had been pulled

up and consumed. Seeds also appeared to be at risk of desiccation, especially those planted into the large blowdown in full sun. Of our 16 seedling plots, 6 accounted for 76% of total germination in the field. The one-quarter of plots in the burned blowdown accounted for only 7% of germination (figure 4.1). Each of the other treatment combinations included some plots that contributed very little and others that contributed disproportionately to total field germination.

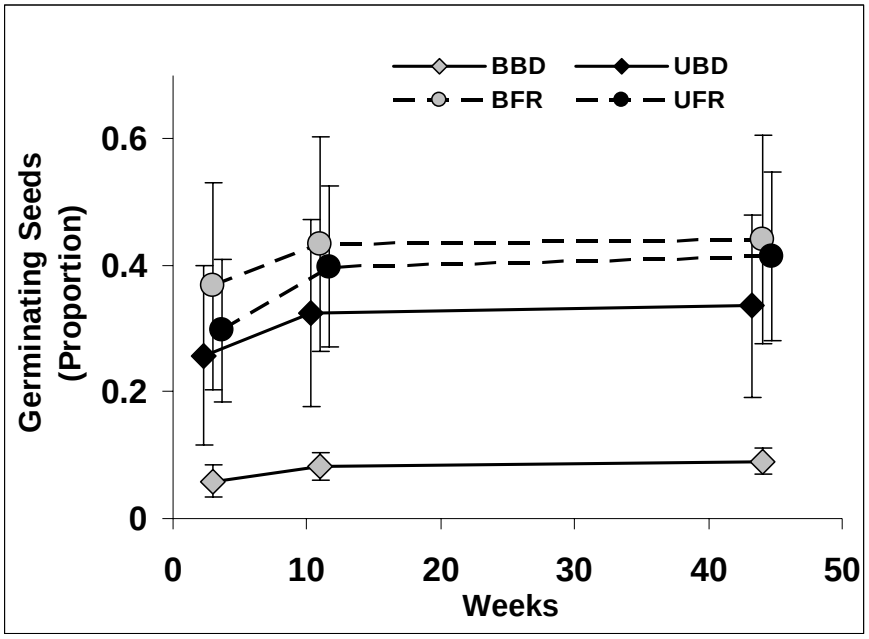

Figure 4.1. Mean cane seed germination during first growing season. Bars represent standard error. BBD = burned blowdown, UBD = unburned blowdown, BFR = burned forest, and UFR = unburned forest treatment combinations.

Experimental treatments had little effect on seedling survival. Plots of mean seedling survival indicate only slight differences between the four treatment combinations (figure 4.2). Statistical analyses of seedling survival similarly indicate that differences among treatment combinations for seedling survival were minimal (table 4.3). In our statistical analyses, among-plot variation again overwhelmed even the time effect (for Transition, $p = 0.08$) (table 4.3).

Overall survival also varied widely among plots in the field experiment. At the end of our two year study, 3 of our 16 experimental plots accounted for 73% of total overall survival

(which combines seed survival, germination, seedling establishment and growth). The next seven plots accounted for 24% of overall survival. The remaining 6 least productive plots (3 of which were in the burned blowdown) accounted for only 3% of total overall survival. The one-quarter of plots in the burned blowdown accounted for only 6.5% of total overall survival.

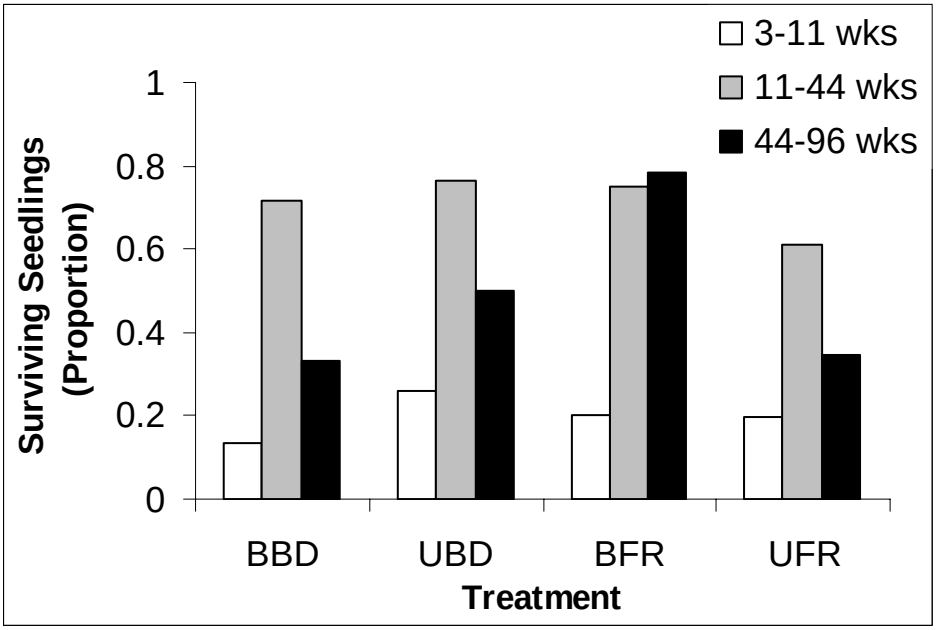

Figure 4.2. Cane seedling survival during three transition periods. Each bar represents the simple mean for the given treatment combination during the given time period. BBD = burned blowdown, UBD = unburned blowdown, BFR = burned forest, and UFR = unburned forest treatment combinations. Data are from four censuses – at 3, 11, 44 and 96 weeks after planting.

Table 4.3. Effects of stand-state, fire, time and their interactions on seedling survival. Survival is modeled as the ratio of live seedlings during current census weighted by those present during the previous census. This repeated measures analysis uses a binomial distribution with logit link in SAS Glimmix Procedure.

Source of Variation:	NDF	DDF	F	*p*
Fixed Effects on Seedling Survival				
Windstorm (forest vs. blowdown)	1	11.09	0.00	0.9520
Fire (burned vs. unburned)	1	11.09	0.03	0.8668
Windstorm x Fire	1	11.09	0.08	0.7771
Transition	2	162.2	2.58	0.0789
Transition x Windstorm	2	162.2	1.36	0.2592
Transition x Fire	2	162.2	1.02	0.3619
Transition x Windstorm x Fire	2	162.2	1.12	0.3285

An examination of mean seedling survival suggests survival varied by time. Survival rates were lowest in the 1–8 week period between censuses 3- and 11-weeks after planting (figure 4.2), suggesting early establishment as a critical stage for cane seedlings. In the third transition, seedling survival was lower overall than in the second transition. Means reconfirm that our windstorm and disturbance treatments had little effect on seedling survival – seedlings performed similarly regardless of experimental treatment (figure 4.2).

Discussion

Our disturbance treatments had only weak effects on germination and no measurable effects on seedling survival. Windstorm treatment alone (i.e., the large tornado blowdown, unburned) had little effect on either germination or seedling survival. We observed that depending on the nearby vegetation, conditions at ground-level could be as shady in the large tornado blowdown as under closed forest canopy. Plots that were burned prior to planting produced fewer germinated seeds, especially in the tornado blowdown (figure 4.1). However, in our statistical analyses this effect appeared to be overwhelmed by high among-plot variability (table 4.1).

The process by which cane produces and regenerates from seed entails several important stages beginning with seed production. Once cane flowers, seed production is in no way guaranteed. We observed cane flowering as individual culms producing no seeds, as many culms within a small area producing few or no seeds, and as thousands of culms from numerous genets covering a large area producing large quantities of seeds. Our tests indicated that more than 80% of the seeds from this mass-flowering event were viable. Woody bamboos are wind pollinated and have mechanisms to facilitate outcrossing (stamens are exserted first, and stigmas

appear after pollen is shed) (Judziewicz et al. 1999). One possible explanation for these observations is that cane flowers are pollen-limited unless multiple genets flower simultaneously.

Many cane seeds do not survive long enough to germinate. Even though cane seeds had no dormancy, in our study, risk of mortality was substantial in the brief time it took them to germinate. We observed that these large seeds were attractive to seed predators, including insects, rodents and possibly birds. Based on low germination rates in our burned x blowdown plots, we suspect seeds were also susceptible to desiccation in dry, sunny environments. Given the risks, we observed an overall germination rate of 35 – 40% for the unprotected seeds in our field study. Germination rates were quite high in some plots and nil in others.

Initial seedling establishment is another stage with high mortality risk. A higher percentage of seedlings died during the eight weeks between our first two censuses than in the ensuing 33 weeks. Of several plots that yielded large quantities of newly germinating seeds (6), half produced virtually no established seedlings, while the other half (3) each produced many. Local environmental factors appear to dictate seedling establishment. We observed that those plots in deep shade wherein many seeds germinated yielded almost no established seedlings. The same was true for low-lying plots subjected to shallow inundation.

We observed that plots with high rates of both seed germination and seedling establishment shared two traits. First, they received partial sunlight at ground-level – seeds rarely germinated in full, intense sun, whereas new seedlings in deep shade typically failed to establish. Second, these plots had a layer of leaf-litter on the ground. We suspect leaf litter facilitated seedling establishment both by hiding seeds from predators and by moderating local moisture and temperature regimes.

Established seedlings appear fairly resilient. Approximately two-thirds of the seeds/seedlings that survived until our 11 week census also survived until our 44 week census (at the end of the following winter). After that, survivorship was lower again during the second year. We suspect this lower second-year survivorship may have been caused by a strong drought that may have also caused high mortality in "adult" cane (see Chapter 3).

Our results suggest that cane seeds are better adapted to partially-open forest conditions than to burned-over areas. If post-disturbance conditions affect the process of seed production and regeneration in cane, it is likely to be prior to seedling establishment. Once established, seedlings handle a range of environments equally well.

CHAPTER 5

CANE ECOLOGY AND RESTORATION IN THE MISSISSIPPI ALLUVIAL VALLEY

Impetus for Cane Restoration

Historically, canebrakes were prominent in southeastern landscapes. When the first European settlers arrived in what is now the southeastern United States, they encountered dense, vast thickets of the native bamboo, "cane" in the bottomlands (*Arundinaria gigantea* Muhl.; Platt and Brantley 1997 and references therein). These canebrakes were widespread throughout the Mississippi alluvial valley (MAV) (Harper 1958). Today, cane occurs only in small sparse stands throughout much of its previous range. Dense and extensive canebrakes have declined by 98%, and this once prominent feature of bottomland hardwood forests is now considered critically endangered (Noss et al. 1995).

Canebrakes furnish critical habitat for numerous bottomland hardwood forest species (Platt et al. 2001). A century ago, canebrakes were known as a refuge for black bears, Florida panthers (*Puma concolor* subsp. *coryi*) and other game species (Roosevelt 1908). Canebrakes are still prime habitat for threatened Louisiana black bears (*Ursus americanus* subsp. *luteolus*). Several migratory birds including woodcocks (*Scolopax minor*), Swainson's warblers (*Limnothlypis swainsonii*) and hooded warblers (*Wilsonia citrina*) use canebrakes (Thomas 1996, Moorman et al. 2002). The rare and possibly extinct Bachman's warbler (*Vermivora bachmanii*) and at least six satyrine (*Satyrinae* sp.) and skipper butterflies (Fam. Hesperidae) are considered cane obligates (Remsen 1986, Brantley and Platt 2001).

Canebrakes can be excellent riparian buffers. In studies of pollution in surface- and groundwater, canebrake riparian buffers outperform mixed-hardwood buffers in reducing orthophosphates, ammonium and nitrates and sediments (Schoonover and Williard 2003, Schoonover et al. 2005, Schoonover et al. 2006).

Ecology of Canebrakes

Cane is the only bamboo native to the U.S. It has been divided into two subspecies (Judziewicz et al. 1999). Switch cane (subsp. *tecta*) is the short-statured (typically < 2 m) subspecies found along the Atlantic and Gulf Coastal Plains. Giant cane or river cane (subsp. *gigantea*) is the larger subspecies, frequently producing culms 5 to 6 m tall and occasionally 8 m in fertile soils. Giant cane is found in bottomlands and along creeks and ravines throughout the southeastern United States including the MAV. Within the MAV, canebrakes occurred primarily on the highest ground along ridge-tops and levies (Platt and Brantley 1997). Today cane can be found growing on virtually any ground not subject to prolonged inundation (Marsh 1977, P. Gagnon pers. obs.). Cane attains its largest size on the most fertile soils. Common lore among early settlers was that the ground growing the biggest cane grew the best crops (Platt and Brantley 1997).

Like many bamboos, cane grows clonally for years to decades before it flowers and dies (Hughes 1951, Judziewicz et al. 1999). How long it takes for a cane seed to germinate, grow to full size, flower and die is not known. The interval may be 20 years or more, which would be typical of woody bamboos (Judziewicz et al. 1999). Cane can flower as individual culms, in small patches, or en masse. Sparse or isolated flowering typically yields little or no seed-set (see Chapter 4.). In contrast, large-scale flowering can produce millions of fertile grains, which sprout the same growing season they are produced (Hughes 1951, Chapter 4). Cane seedlings are inconspicuous and resemble many small understory grasses (Hughes 1951, and P. Gagnon, pers. obs.). Juvenile cane plants grow for several years before culms attain full-size (P. Gagnon, unpublished data).

Cane is a giant grass. Stands of cane inevitably decline in the deep shade of closed forest canopy, although sparsely distributed stems can persist for years in such an environment. Cane

stands need at least partial sunlight to maintain dense, canebrake-like structure (see Chapter 2). Culms of giant cane grow tallest in shade. They are shorter but grow more densely in full sunlight (Chapter 2). Hughes (1957) concluded that stands of switch cane (subsp. *tecta*) in North Carolina gradually declined in density after several years of vigorous culm production, and stands of giant cane in the MAV appear to follow a similar pattern (P. Gagnon, unpublished data). This decline can be avoided or reversed if cane is periodically burned (Hughes 1958 and see Chapter 3).

Ecological disturbances appear to dictate much of cane's clonal growth. Natural and human-caused disturbances are prevalent and diverse in the MAV. Tornadoes, hurricanes, violent thunderstorms and ice-storms all knocked down forest canopies. Flooding from the Mississippi River and its tributaries damaged forests, as did flooding from beaver dams. Fires (whether natural or anthropogenic) also occurred occasionally. With its capacity for rapid clonal growth, ability to persist in shade, and preference for higher-light environments, cane could potentially exploit virtually any forest gap in the MAV on non-inundated land regardless of the type of disturbance that generated it.

Restoring Canebrakes

There are essentially three possible pathways for restoring canebrakes in the MAV. The first way is to restore already-present but sparsely growing cane. The second is via vegetative propagation – full-sized cane or rhizomes can be transplanted from another location. The third is to plant cane from seeds collected elsewhere.

Canebrake restoration can be straightforward when diffusely-growing cane is already present. The cane may only need a more favorable environment to form dense thickets. At least partial sunlight is critical for development of cane thickets. At best, cane growing in deep shade

will persist for years as occasional, sparsely-distributed stems. In such cases, thinning the overstory can promote the growth of higher-density cane stands. Cane is somewhat shade tolerant, and on a favorable site it can grow into high-density patches in the forest gaps commonly left by uneven-aged silviculture (Chapter 2). Expansive canebrakes, however, require large canopy gaps or a sparsely stocked overstory.

Increased light alone will not ensure the formation or persistence of canebrakes. Hughes (1957) reported that stands of switch cane naturally senesced after a period of years, and a study of giant cane in the MAV yielded a similar result (Chapter 3). Hughes (1957) suggested burning stands of switch cane at intervals of 7 to 10 years to maintain them at high density. Giant cane in the MAV likewise benefits from this treatment (Chapter 3). Fire simultaneously stimulates vigorous resprouting of new cane culms, returns nutrients to the soil, and reduces competition from other plants. Where cane stand density is too sparse for fire to spread naturally, or where natural fires are likely to be outside of management prescriptions, cane can be cut, dried in place for a week or two, and then burned (P. Gagnon, unpublished data). Where prescribed burning is not feasible for reasons of policy or logistics, cutting cane without burning it may offer some, though not all, of the benefits of burning (P Gagnon, pers. obs.), though this has not been tested experimentally. A combination of overstory thinning and periodic prescribed fires should maximize cane vigor and stand density.

Where cane is not already present on a site, it can be transplanted from elsewhere. This method of canebrake restoration has met with mixed results. One experienced source who has overseen both failed and successful cane transplantations suggests that rhizomes be transplanted as large root wads (30-45 cm in length) with as much intact soil as possible (Kelby Ouchley, personal communication). When transplanting root wads, Ouchley urges that great care be taken

to avoid introducing invasive competitors. Even well-established cane can be drought sensitive (P Gagnon, unpublished data). Transplanted cane will survive and establish better if irrigated during dry periods. Reliable establishment from rhizomes may take 2 or more years. Ouchley speculated that difficulty establishing cane on reclaimed agriculture fields may result from the absence of a critical mycorrhizal symbiont. More research on this aspect of cane biology is needed.

One cane restoration project in Missouri used cane transplanted in two-gallon root wads. After two years, the cane had established and was spreading, despite substantial competition from vines (Shively et al. 2002). Each transplanted root wad originally had 1-4 attached culms. Some were treated by cutting off all culms prior to transplanting. These produced fewer new culms and were less likely to survive than those transplanted with culms intact. Cane growth accelerated in the year after a flood temporarily inundated it under as much as 4.5 m of water. The authors speculated that cane growth accelerated because the flood reduced vine competition.

Cane can be transplanted as individual rhizomes if treated appropriately. A series of studies in southern Illinois used cane rhizomes cut into lengths of 20-30 cm, planted into greenhouse pots and misted frequently with water (Zaczek et al. 2004, Hartleb and Zaczek in press). After one month in the greenhouse, more than three-fourths had sprouted at least one culm. Rhizome segments with 10 or more nodes sprouted more culms than rhizome segments with fewer nodes. Rhizomes collected in early spring outperformed those collected in either fall or late winter, but fall- and winter-collected rhizomes still sprouted frequently. When transplanted to restoration sites, culms from these sprouted rhizomes had established and spread substantially after 3-4 years. Although competition from other plants reduced cane growth after transplantation, pre-treating the restoration site with herbicide to kill competitors did not improve

cane success. In the study, establishment success varied significantly by both donor sites and transplantation sites. After testing several transplantation methods, Zazeck et al. (2004) determined that the best method was to plant each rhizome distal-end up, with multiple nodes and buds above ground level and exposed to light. Using this method, sprouting rates exceeded two-thirds even for rhizomes stored for one month in moist refrigeration. Nevertheless, successful transplantation is possible even without first sprouting rhizomes in a greenhouse (J. Zaczek, pers. com.).

Successful establishment of transplants is only the first step toward full canebrake restoration. As described above, established cane requires at least partial sunlight and periodic disturbance to attain dense, "canebrake-like" stand structure. Eventually, long-term re-establishment of cane on a given site will require successful flowering and seed production. Existing evidence suggests that out-crossing may be necessary for successful seed set. Long-term restoration success from transplanting may require that multiple genetic individuals be transplanted into the site, and eventually flower in-phase years later.

Finally, cane can be reintroduced from seed. Cane flowers infrequently, and procuring a large quantity of viable seeds may require some luck and good contacts to discover where cane is fruiting abundantly. Occasionally cane can be found flowering en masse. These events may produce millions of plump, fertile grains in the late spring. Instead of producing the usual flush of new leaves in the early spring, flowering cane will appear straw-brown as though dying. Upon closer inspection, flowering culms will be covered with inflorescences resembling heads of rice or wheat. In Louisiana, cane seeds ripen in late April or early May. This timing may be later farther north in the MAV. Cane seed-heads progress quickly from green to ripe (P. Gagnon,

pers. obs.). Once ripe, heads shatter easily and drop seeds in even a slight breeze (Hughes 1951), so frequent monitoring of flowering patches is necessary if collecting ripe seed is a goal.

Cane seeds can be planted by pressing them lightly into moist soil. Cane seeds have no dormancy, and the best germination rates result from planting soon after seeds are harvested (P. Gagnon, unpublished data). Even so, some seeds should remain viable for a year or more if sealed and refrigerated. In one instance, 50% of seeds sprouted after 18 months in refrigerated storage (M. Cirtain, unpublished data). Chances of germination are maximized by planting seeds into leaf litter in partial shade (P. Gagnon, unpublished data) in moist, well-drained soil (Cirtain et al. 2004). Seedlings can also be started in a greenhouse and then transplanted out the following growing season (Cirtain et al. 2004). Seedlings are susceptible to drought and do best in soil with substantial organic material (P. Gagnon, unpublished data). Accounts differ whether cane seedlings benefit from fertilization (see Hughes 1951 and Cirtain 2004). Growth of cane seeds into adult plants is undocumented, but most bamboos require 3-7 years to reach full size (Judziewicz et al. 1999), and cane appears likely to follow a similar pattern (Hughes 1951 and Chapter 4). Without careful monitoring, cane seedlings are inconspicuous, and positive results may require five or more years to manifest. Planting a large number of cane seeds may be the best way to ensure long-term canebrake restoration. The seedlings will grow up as a cohort and should be in-phase for flowering when that time comes years later. Cane seedlings are somewhat shade tolerant, but to attain dense stand structure they will need at least partial sunlight and periodic disturbance as they mature.

CHAPTER 6

CONCLUSIONS

General Implications

This dissertation explores the effects of windstorm and fire disturbances on cane clonal and reproductive biology. In this collection of studies, multiple disturbances interact in complex ways. Some of these interactions appeared only after a substantial time lag. Results indicate that disturbance histories affect plant responses to subsequent disturbances. In the case of fire, plant dynamics have the potential to influence disturbances just as disturbances can influence plant dynamics. One implication of this research is that interacting multiple disturbances might strongly influence the interplay between monodominant and species-rich plant communities.

Multiple Disturbances and Cane Clonal Ecology

Like all woody bamboos, cane is a giant grass and a highly clonal organism. Cane rhizomes branch and grow below-ground and can span several meters between above-ground culms. At our fieldsite a large majority of culms sprout during mid-summer (late June through the end of July). Culms attain full size in just a few weeks after sprouting from rhizomes, after which they grow no more in height or diameter. Culms frequently live 5 to 10 years (Hughes 1957). Culms are composed of multiple node and internode segments. Culms typically branch once or twice per node during their first growing season, and these in turn branch at the start of each subsequent growing season (Hughes 1957). In this way, approximate culm age is reflected by the number of times a culm has branched (Chapter 2). Open-grown culms are relatively short; culms grow tallest in fertile soil in shade (Hughes 1957). Whenever a cane stand is burned or cut, new culms are typically shorter than their predecessors, and then each subsequent year's culms are taller on average than those from the previous year (Hughes 1957).

The effect on cane of a windstorm that opens a large forest gap is accelerated new culm production for cane stands in the gap (Chapter 2). As a result of faster culm production, ramet

density (i.e., number of culms/m^2) increases in open-grown cane stands compared with similar forest-grown stands (Chapter 3). Over the course of this four-year study, ramet populations increased in a large tornado-generated gap, were essentially in stasis in small stands growing under forest canopy, and declined in the large, continuous stands growing under forest canopy (Chapter 3). Cane appears to spread outward regardless of above-ground ramet density (Chapter 2). These results suggest that cane stands might actually shift location over time as small forest gaps form and close (Chapter 2).

The effects of fire on cane are complex, and some may be lasting. In the year of fire, populations of burned cane ramets grew faster than unburned populations in the large tornado blowdown gap (Chapter 3). In forest, populations of both small and large cane stands declined in the year of fire, but growth rates rebounded in the year following fire (Chapter 3). All unburned ramet populations declined during the final year of the study, perhaps because of a strong drought that year (Chapter 3). In contrast, previously burned populations during that same year grew or were in stasis (Chapter 3). This suggests that burning cane may impart resistance to subsequent environmental shocks (Chapter 3).

Together, these findings suggest how a sequence of multiple disturbances might promote natural canebrake formation. The first step in the sequence is for a large storm (hurricane, tornado, ice storm, etc.) to create a large forest gap where cane is growing. Cane stands will increase in ramet density as they spread outward (Chapters 2 and 3). As they do so, separate cane stands may grow together into larger stands. Over a few years, the large gap will fill with dense vegetation. The next step in the sequence is for wildfire to occur in this large blowdown. Such a fire could damage surrounding forest trees, thus increasing the size of the forest gap. Once burned, cane stands in the blowdown will grow at a faster rate, and the young culms in

these stands may be more resistant to environmental shocks (Chapter 3). As separate cane stands continue to spread, they will amalgamate to form canebrakes. These denser burned cane stands might also be more pyrogenic, increasing the likelihood of subsequent fires, which would in turn promote cane's dominance of the site (Chapter 3). Although anthropogenic fires might further facilitate canebrake formation, this sequence of events could also occur naturally in much of the southeastern U.S., where powerful storms are common and lightning strikes numerous. The counterpoint to this scenario is that without periodic disturbances, cane will decline over time. Cane could be extirpated from second-growth forests where canopy gaps are rare and fires non-existent.

Cane Reproduction and Regeneration

Disturbance effects on cane reproduction and regeneration appear most likely during seed survival and germination. Cane flowering events range from lone culms, to many culms locally, to thousands of culms over a wide area (Chapter 4). Seed production may be most likely when multiple genets flower synchronously (Chapter 4). Windstorm disturbance had little effect on cane seed germination and seedling survival – seeds and seedlings in blowdown and forest conditions performed equally well (Chapter 4). Cane seeds planted into burned areas (especially burned blowdown areas) were less likely to survive and germinate, although strong among-plot variability make this result weak (Chapter 4). Once germinated, seedlings in blowdown and forest survived similarly well (Chapter 4). There appear to be three critical stages in the process of cane reproduction and regeneration, including seed production, germination and seedling establishment (Chapter 4). Once seedlings are established, survival rates are higher. Cane seeds/seedlings germinated and survived best in partial sun planted into a layer of leaf litter

(Chapter 4). These results suggest that cane seeds are adapted to life in partially-open forest conditions.

Cane Restoration

These results inform cane restoration efforts. When cane is already present onsite, cane growth can be encouraged by ensuring the forest canopy is sufficiently open (Chapters 2 and 5). Period burning (every 5 to 10 years) will improve vigor of cane stands (Chapters 3 and 5). Full canebrake restoration will probably require a plan that mimics the sequence described above, by which canebrakes might have formed naturally (Chapter 3). Where cane is not present, it can be transplanted from rhizomes. These can take the form of either rhizomes with root wads intact, or of rhizome segments sprouted in a greenhouse and then planted with distal end up (Chapter 5). Cane can also be restored by planting seeds. Although seeds may be a challenge to procure in adequate numbers, regeneration from seed may be the best way to ensure that multiple genets grow-up in-phase at time of flowering years or decades later (Chapter 5). Our results suggest cane rhizomes and seedlings may be susceptible to drought until well established (Chapter 3).

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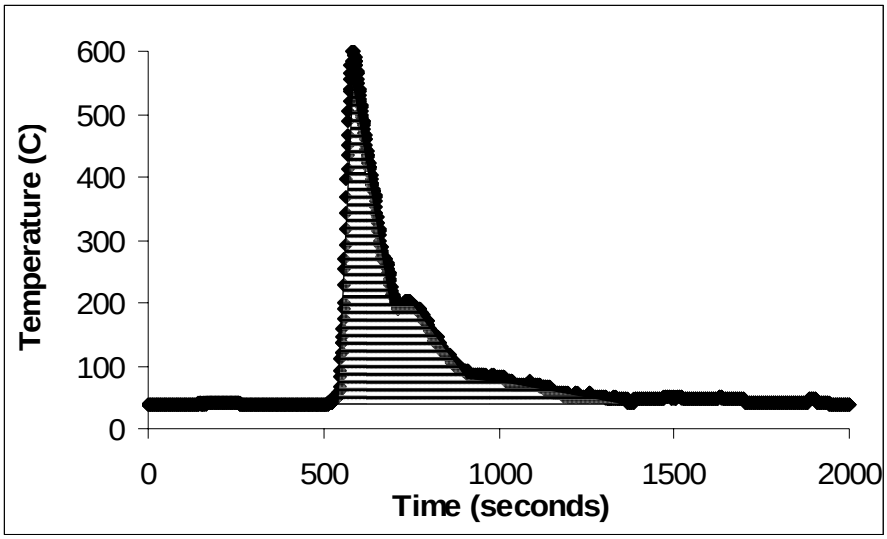
APPENDIX A

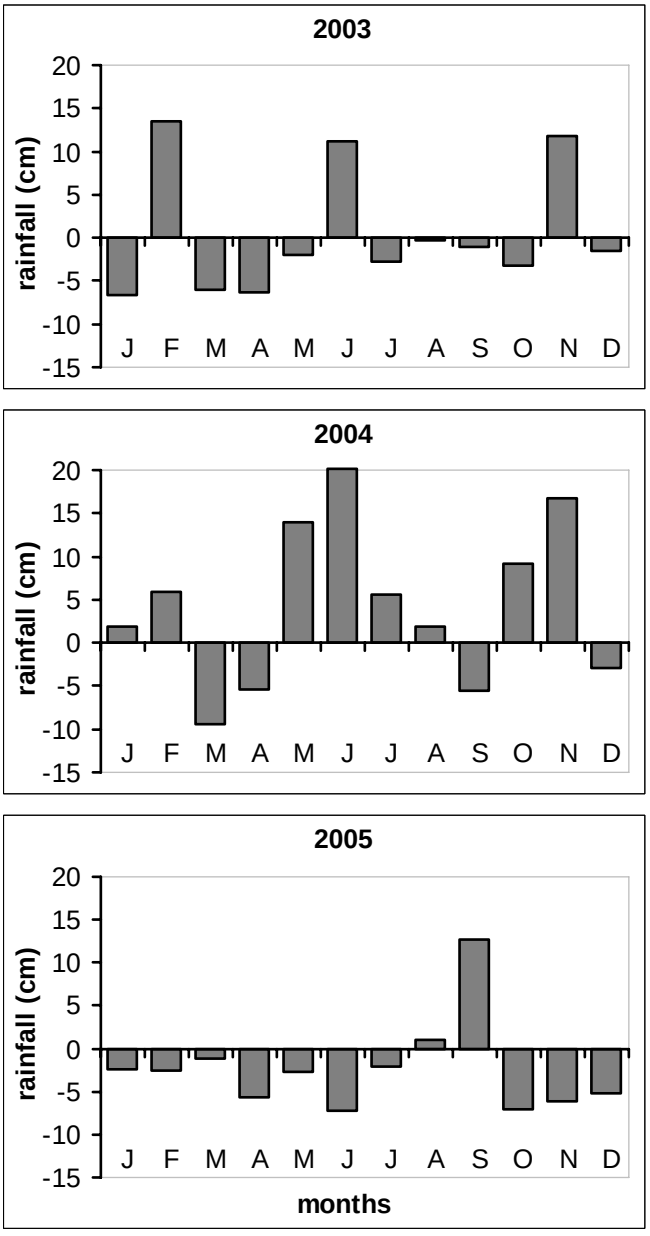
TOTAL TEMPERATURE INCREASE



An example time-temperature curve from a burned subplot. Fireloggers measured temperature at one-second intervals. Total temperature increase is the area under the time-temperature curve (the striped area), calculated by summing all temperature readings for a particular subplot together, less ambient temperature.

APPENDIX B

DEVIATION FROM MEAN MONTHLY RAINFALL



Monthly rainfall in Tensas Parish, LA compared to mean monthly rainfall during the three transition years of 2003, 2004 and 2005. The x-axis represents the 12 months of the year. The y-axis represents the deviation of that month's rainfall from the historical mean rainfall for that month, measured in centimeters.

VITA

Paul R. Gagnon was born in Dallas, Texas, on May 1, 1968, to J. Roger and Margaret Gagnon. He grew up in Ennis, Texas, where he attended St. John Elementary and High Schools. His passion for ecology began during a childhood spent chasing critters, hunting and fishing. He attended college at Baylor University in Waco, Texas, and graduated with a bachelor of arts in economics and business in 1990. He joined the Peace Corps and served two years as an aquaculture volunteer in Togo, West Africa, where he learned French. After completing his service, he spent six months traveling through Africa and Asia, then worked as a recruiter for the Peace Corps in the Southwest Regional Office in Dallas, Texas. After eighteen months, he left to travel in Latin America before attending the Yale School of Forestry and Environmental Studies in New Haven, Connecticut. He completed a master of forest science degree in 1998, including a thesis on ethnobotanical lore of the descendants of African slaves living in a mangrove forest in northwest Ecuador. In 1999 he entered the Department of Biological Sciences at Louisiana State University, where he did his doctoral research on disturbance ecology of a native bamboo under the supervision of William J. Platt. He plans to pursue a career in ecological research.